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# THE AMERICAN NATURALIST

A BI-MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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EDITED BY JAQUES CATTELL

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WITH SPECIAL REFERENCE TO THE FACTORS OF EVOLUTION

VOLUME LXXIX

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# THE AMERICAN SOCIETY OF NATURALISTS

## SOME PROBLEMS OF HUMAN RACIAL DEVELOPMENT AND MIGRATION[1]

PROFESSOR FAY-COOPER COLE
UNIVERSITY OF CHICAGO

I HAVE been asked to discuss "Some Problems of Human Racial Development and Migration" in the space of a half hour. I once had a professor who urged "take time to be brief," but there are so many angles to this subject and it covers so much time and space that the best I can hope to do is to indicate a few of the problems.

My difficulties begin when I use the term *human*. Where is the dividing line between prehuman and human? Just about the time of the Dayton trial came the discovery of Australopithecus. A London journal came out with an illustrated article calling this the oldest find of fossil man in Africa or perhaps in the world. American papers copied and one of our British colleagues was so fearful I might use the material in my testimony that he sent me a long message saying the find was not man but an ape far advanced toward man.

How human does a "man-ape" have to be before we class him as human? Does the distinction lie in cranial capacity? If so, the six-year-old Australopithecus had already passed out of and beyond the range of Anthropoid apes of like age.

Is it in proportions of the brain? If so, this youngster showed very human traits in the high degree of development of parietal bosses and in expansion in the temporal

[1] Address of the retiring president, American Society of Naturalists, Cleveland, Ohio, September 14, 1944.

portions. Or is it in teeth? Here the baby teeth show intermediate characters.

Probably we would agree that we must use a complex of traits in making the distinction between man and the apes.

At the time Australopithecus was found it was considered as probably Pliocene in time! Now in the same area of Africa we have closely related adult forms which come so far into Pleistocene that it is clear we are dealing with a line of apes that never quite arrived. They present a far development or experiment toward man, but for some reason died out without becoming *homo*.

But what is *homo?* When the much disputed teeth, skull cap and femur of *Pithecanthropus erectus* were first examined by a group of specialists, part said that if all belonged to one individual he was a primitive type of man; others said "giant baboon" and still others said "an intermediate form—an erect ape-man." The additional discoveries of Dubois and now the materials offered by von Koenigswald and Oppenooth—jaws, more teeth, additional femora, three adult and one baby skulls—leave us in no doubt that we are dealing with man. We have a complex of traits falling closer to man than to apes.

The closely related Sinanthropus forms found in China are likewise accepted as fossil men and here an additional claim is added—the use of fire and possession of tools. Can we use evidences of man's intelligence and creative ability in our attempts to classify?

Another set of questions is raised when we inquire of the time and place of man's arrival. By referring again to teeth and fragmentary jaws we can say that beings possibly ancestral to man and the Anthropoid apes had appeared in Miocene times in India and in Europe. We can go further and say that the flora and fauna with which the Sivapithecus beings of India were associated extended toward Europe and across India and Burma to the southeast as far as Java—thus extending the probable range of these "ancestral" forms. It is important to note that in later horizons we find Pithecanthropus at one

end of this range while at the other end, in Europe, claims for early man are set up by the discovery of Heidelberg, Piltdown and Swanscomb. Man at both ends of this arc but no equally ancient finds in between.

Where are the evidences of the developing forms which must have spanned the interval between Sivapithecus, Dryopithecus and the human forms just mentioned?

To-day it s generally conceded that Pithecanthropus is not earlier than second interglacial—perhaps later—while no fossils from Europe or Africa can lay clear claim to an earlier birthday.

A vast time interval extends between these possible ancestral forms of Miocene times and the first forms on which we can agree as being man.

For more than three decades Pithecanthropus stood alone in Asia in the battle with the fundamentalists. During that period some came to doubt the reliability of his teeth; others insisted that the very straight femur never supported the very primitive skull cap, and—unkindest cut of all—his discoverer came to class him as a giant gibbon. Then came the new discoveries. Cast doubt on any single feature or combination of features of Pithecanthropus, and the recently excavated materials rise to confound you.

Still more convincing are the additional discoveries in this part of the world. Toward the end of Tertiary times the easy line of movement between India and Java seems to have been broken and we no longer speak of the Siva-Malayan fauna. In its place comes the Sino-Malayan, which extends from Java to Pekin. Now with the Sinanthropus finds we have early fossil man of nearly the same time period at both ends of *this* arc.

Sinanthropus and Pithecanthropus seem much alike, yet because of the circumstances surrounding the discovery and description of the first Sinanthropus tooth we are confronted with a new genus and species. Should we continue to recognize similar forms under diverse names because of historical accidents, or should we accept

recent suggestions and call the Chinese finds *Pithecanthropus pekinensis?*

Claims for second interglacial man in Europe are fairly well substantiated by the finding of man-made objects in the strata of that time. It also seems possible that the famous Heidelberg jaw belongs to this period. Of this jaw we need only say that except for size it seems directly in line with the jaws of the later Neanderthalers.

Another find sometimes assigned to this period is Piltdown. The whole subject is so filled with question marks that most students of human history are in doubt whether we should bless the painstaking efforts of Charles Dawson, who recovered the fossils, or should berate him for dragging this skeleton into the family closet.

The deposit in which the materials were found is an alluvial fan claimed by some to be second interglacial, by others as third glacial. Some of the materials washed in are doubtless from Tertiary deposits but others belong to the last stages of the formation.

Workmen taking out materials for road repairs turned up pieces of a human skull. These came to the attention of Mr. Charles Dawson, who, in company with Sir Smith Woodward, carried out the search which resulted in the much disputed fossil. The workmen's pit extended four feet into the gravel and it was from this level that the crushed fragments of a woman's skull, half of a lower jaw, two molar teeth and a canine tooth and nasal bones were taken. With or below the skull was a bone tool cut to a rude point from the leg bone of an ancient type of elephant (Meridionalis), also some crude stone chips.

The skull and jaw do not bear evidence of having been water carried, as is the case of the tertiary bones in the deposit. They are badly crushed, but it is not certain whether this was due to ancient causes or to the workmen. They lie so shallow they could be intrusive from above—a suspicion which is strengthened by the association with the bone utensil and eoliths. On the other hand they appear, in color and stage of fossilization, to belong to the deposit.

Finally we come to the fossil itself. The bones of the cranium are unusually thick and there are some other hints of primitiveness, but taken as a whole the skull is very modern. It even lacks a suggestion of the huge supraorbital ridges which characterize Neanderthal and the early Asiatic finds. Yet the jaw appears to belong to a fossil chimpanzee, and this is further confirmed by the teeth.

The combination of an advanced skull with an ape's jaw proved too much for many scientists, yet a second find of portions of a skull and a lower molar of the same type as with the jaw does give aid and comfort to the reconstruction called *Eoanthropus dawsonii.*

The skull and jaw may belong to the same individual—a difficult situation even for asymmetrical evolution to explain. The association may have been fortuitous—a hard thing to explain in view of the second find. We may be dealing with a burial of modern man, who by chance was placed in a deposit containing the jaw of a fossil chimp. But no other fossil chimpanzees have been reported from England.

All this is bad enough, but now appears a group of scholars which argues that Piltdown is an early representative of *Homo sapiens* who had reached England as early as or earlier than the Neanderthalers.

To strengthen their claim they point to the very modern skeleton of Galley Hill man, to the fragmentary skulls found at London and St. Edmunds, to the east African discoveries of Leaky and finally to the Swanscomb fragments. Each and all of these are in question either as to the age of the deposits in which they lie, or as to their assignment to *Homo sapiens.*

Frankly we don't know what to do with Piltdown man—who by the way is a lady—we can't dismiss her—him—and we can't accept her credentials. We agree with Howells when he says that Piltdown has scotched more attempts to draw up a family tree for man than all the other fossils put together.

The story of Neanderthal man during the fourth and last major glaciation is well known. We know a good deal about his life and his physical type. It had long been suspected that he occupied Europe during the third interglacial, and the very Neanderthal-like jaw of Heidelberg suggested that his ancestors had appeared there by the second interglacial.

Recent discoveries show Neanderthaloids at Ehringsdorf, at Steinheim and near Rome in third interglacial. Part of the Mt. Carmel people likewise indicate a Neanderthal element in Palestine at this time, while the very Neanderthal-like people known as *Homo soloensis* recently discovered in Java, along with other finds, make it clear that man conforming rather closely to this type was widespread over Europe, Asia and possibly Africa by the end of the third interglacial.

But was he the only human of that period, and if so what of the ancestry of *Homo sapiens?* We have already noted the very questionable family tree built up through Galley Hill, Swanscomb, Piltdown and Kanjera series.

You all recall the dispute between Drs. Hrdlička and Elliott Smith following the Huxley lecture of 1927. Hrdlička indicated that *Homo sapiens* had developed directly out of Neanderthal, perhaps in Europe. Smith was firm in his rebuttal.

Just how closely are we related to Neanderthal?

The Steinheim skull, of early third interglacial, is accepted as Neanderthaloid, yet in skull height and more retracted face shows development toward later man. If Swanscomb isn't *Homo sapiens* then he shows development in that direction. The discoveries of Garrod and McCown in Palestine seem to indicate that *Homo sapiens* had already appeared and had intermixed with Neanderthal, or we are there dealing with a group recently branched off from that parental stem.

Another hint of what was going on about this time is supplied by the recent finds in Java. *Homo soloensis* is probably late third interglacial; he certainly is very Neanderthal-like. He may be descended from Pithecan-

thropus; he probably is ancestral to the later Wadjak fossils. These seem to tie up with the fossil finds in Australia and thus to the modern Australoids. But the Australians are *Homo sapiens*. The evidence is not absolute, but the hints are clear that Neanderthal may be much more closely related to us than we have been accustomed to think.

The appearance of Cro-Magnon in Europe during the waning of the last glaciation is ample evidence that man of our species had undergone a long period of development and specialization outside Europe and that he entered as a well-defined physical type quite different from Neanderthal.

That the classical Cro-Magnon with his large stature, long-narrow-high head and short, wide face was not the only representative of the species is clearly demonstrated by the discovery of the Grimaldi skeletons, the appearance of Brünn man and the variant types of skulls found at Oftnet and Mugum.

Apparently the question of sub-species and race is raised as soon as *Homo sapiens* is definitely known.

When I chose this topic I had expected to devote half my time to the modern races. Now my time is nearly finished and I have only alluded to modern man.

We can excuse our uncertainty regarding the fossil record by the scanty nature of the evidence, but problems do not cease as the evidence accumulates.

We accept the idea that all living groups of mankind belong to one and the same species and that the separation into sub-species and races probably goes back toward the end of the Pleistocene. The ways of classifying still lead to some confusion, but I believe the majority will accept the scheme whereby the species is first divided into three main stocks or sub-species—Negroid, Mongoloid and Caucasoid—and these are further subdivided into races, subraces and so on down.

For such a classification we must use a large number of traits to distinguish each division; putting together those who are alike and separating them from those who

differ. We assume that certain traits—such as the curly or frizzly hair, broad flat nose, projecting face and everted lips of the Negroids—are old and entrenched and thus serve to distinguish them from Caucasoids and Mongoloids. But inside these divisions other groupings appear which serve to set up the races—such as Nordic, Alpine and Mediterranean. They possess most of the distinguishing traits of the Caucasoids and in addition have still others probably of more recent origin.

The probable causes of change are familiar to all—mutations, isolation, inbreeding, natural and social selection, possible effects of environment and so on. Here it need only to be recalled that archeology shows us that until the development of agriculture and animal husbandry, mankind was in small hunting and seed-gathering groups, much on the move. Under such conditions variant forms had a much greater chance of becoming established, while natural selection worked more drastically to eliminate those unfit for the conditions under which a group was then living.

Granted all this there are still many unsolved problems. For instance, most people think of Africa as the homeland of the Negro. But large and small Negroes are found not only in Africa but in New Guinea on the other side of the world. Traces of this people occur in the present populations or in archeological horizons along the coasts all the way between. It is extremely unlikely that environmental conditions at the two peripheries could independently produce the complex of traits by which we define the Negroids. There is much to suggest that, with the possible exception of the Bushman, all the Negro groups are rather recent intruders into Africa. If this is true we should perhaps look for origins somewhere toward north India.

We may imagine a time when the various isolated Caucasoid races were relatively pure and we can trace their movements with some assurance from the general region of the Aral-Caspian seas toward Europe, Asia and

India. Mutations reinforced by natural selection may have established a blond grouping in the Baltic area, while reverse conditions may account for the dark skin color of the Aryan speaking peoples of North India, who are otherwise close to the Mediterraneans.

The dividing line between the round-headed Alpine Caucasoids and the western Mongoloids raises questions of relationship other than race mixture.

With race mixture our problems really begin. Mixture is old and in many regions is very thorough. It has come about through migrations, invasions, war, slavery and countless other causes.

One group urges against mixture—especially of very diverse races. Claims of resultant sterility, of production of monsters, of lowered quality of body and intellect are met with equally valid evidences of hybrid vigor, of increased fertility and of superior physical types—due to mixture.

Biologically, race is an established fact, and this leads to claims for superior and inferior, for innate characters of race and so on. Such claims are dubious, but human attitudes do affect the mental and cultural development of whole groups.

Those of you who deal with other animals don't realize how fortunate you are. You can put your subjects into a cage; you can control their mating and you can watch results over several generations. No such happy situation faces the student of man. He is a slow breeder; he refuses to conform in his mating habits; and you can't lock him up for long. Paleontologists may say "if these bones could only speak," but if we judge by living man, most information on racial matters that the talking bones would give would be misinformation.

I have exceeded my time. I have only begun to touch on problems, but fortunately these are problems raised by increasing knowledge concerning man. A century ago speculation was rampant—to-day at least we have enough information so we can ask questions.

# BIOLOGY AND HUMAN PROGRESS[1]

## BIOLOGY AND THE PUBLIC MIND

PROFESSOR C. V. TAYLOR
STANFORD UNIVERSITY

THE general topic proposed for our discussion to-day, "Biology and Human Progress," is a significant departure for these annual symposia of this time-honored Society of Naturalists. That departure is evidently in keeping with the tone and spirit of other sessions of the association this year and is, of course, amply justified.

Momentous world events, that are uppermost in the minds of men everywhere, continually remind us that this is a grave, crucial period in man's long, eventful, perilous history. A complacent view of our species history might be that having thus far managed somehow not only to survive but also slowly to gain dominion over the earth, the sea and the sky, we may be assured that nothing can ever finally prevent man's further progress.

The stark fact is, however, that twice within the memory of those here to-day, the nations of the earth have again repeated mankind's warring history, have again resorted to armed force as the means of deciding human issues, of solving human problems. And we are now well aware that for cost in lives and treasure, for sheer brutality and utter devastation, the five years now of this second World War have far surpassed that of World War I and so of any war of recorded history.

Lloyd Stratton, veteran of the last war and now chief of the British Associated Press, recently wrote from the Normandy bridge-head: "I saw nothing massed on the Western front in 1918 that in magnitude and power equalled that now concentrated on this small Normandy

[1] Papers from a symposium presented at the meeting of The American Society of Naturalists during the sessions of The American Association for the Advancement of Science at Cleveland, Ohio, before a joint session with the American Society of Zoologists and the Botanical Society of America, September 14, 1944.

front. In the Caen area and around St. Lo, are towns as totally destroyed in one brief all-out offensive as occurred in the previous war after three years of back-and-forth fighting.''

We over here can read such items and hear such reports, yet we can not grasp their full import. Fortunately for us, we are too far away from it all, in a fortunate land now made secure from the death and devastation of other war-stricken peoples and lands. Fortunately, perhaps, we can learn only through others of these depths of man's inhumanity to man—of entire cities that are being blasted out of existence, including monuments of man's finest handiwork and libraries of man's recorded progress and best thought. These things, once posterity's choicest, rightful heritage, that represented even centuries of development, of saving and of honest toil, are now only rubble and ruin. Truly these are damaging indictments of man's boasted rational behavior.

And, as if these were not indictments enough, we have also to reckon the future effects of this earth-sweeping storm which assuredly carries in its wake enormous impacts and repercussions, the full outcome of which none of us would scarcely dare predict. From these impacts, however, we may be equally sure that no man, woman or child, here or elsewhere, who survives this struggle, can possibly escape. Nor can we imagine an end to its deeper repercussions short of many generations to come. Indeed, recognizing that only the best of younger men these days can meet the requirements of war, we here well realize that of those who are sacrificed without issue, their hereditary, as well as their individual, potentialities are lost to our species forever.

In the face of such world events and of their certain aftermath, what now can we as American scientists, as American naturalists, say regarding future human progress? It ought to be fortunate, for others as well as ourselves, that America is far removed and is made safe from the seething centers of this world holocaust. What might fellow scientists in those centers say, or have a right to

say nowadays, even at the very mention of human progress? Our situation, accordingly, affords an opportunity, and it imposes an obligation, to try to view mankind's awful plight with better perspective and more objectivity. This would, of course, be our customary procedure in approaching our usual scientific problems. May not a similar approach, let us say a biological approach, be attempted also on some of our urgent, baffling human problems? To be sure, such efforts would not be new, and various past efforts may have been more effective than we can well realize.

Our symposium to-day was evidently conceived and planned with that hopeful prospect in view. Professor Sinnott's paper will have to do with the promising extraordinary contribution that plants can further make to the material basis of our civilization. All of us can readily sense the import of that theme and are now looking forward with great interest to his discussion. The other paper by Professor Chambers, on the rehabilitation of our fellow scientists in the occupied, war-ravaged countries, presents an obviously human problem, the urgency of which needs no comment. What may best be done in their behalf and how that may promptly be done affects each of us directly and deeply.

My own discussion to-day on "Biology and the Public Mind" may be prefaced as follows: Recognizing civilization as a relatively recent human institution, whose superstructure requires, to maintain stability and growth, a stable foundation, it is suggested that biology can continue to contribute to a better understanding of both the superstructure and the foundation. To that end, it is further apparent that in the future, more than in the past, the added task of biologists will be to clarify accurately in the public mind the biological nature of civilization as essentially an expression of the biological nature of man.

It may here be agreed that the known relatedness of biological nature and human nature, the latter being an extension of the former, has not been adequately exploited, especially in the interests of a better-informed

public. Reasons for this seem obvious, for in that endeavor we are at once confronted with certain limitations which are in part traditional, but also they are partly of our own making. Traditionally, they relate to common misconceptions, even in the otherwise informed public mind, about both our scientific method and our scientific system of knowledge and understanding. Science in general has come to be compartmentalized within a given field or fields and barred from other fields. We might recall, in this connection, that naturalists are, by one definition, versed in the natural science of plants and animals—to the exclusion, presumably, of the natural science of man. But such distinctions are not confined to the lay public. We are all familiar with the current view, which seems to be widely reflected in our universities these days, that the departments of human knowledge are in the main mutually exclusive in both their materials and their methods. This obtains especially, it is said, for the natural sciences on the one hand and the humanistic studies on the other hand. Science, accordingly, has not the competence for the solution of human problems. Human qualities are intrinsic qualities that have no essential counterpart in other living things. Scientific tools and procedure have gone far in the analysis of stars and atoms, of vitamins and cells and fruit-flies. These methods evidently are adequate in the quest of nature around us, but they leave the nature of man unapproachable.

Such common misunderstandings of the achievements and capacities and the province of science may come to be even more accentuated after the war, not only in the public mind but perhaps also in our colleges and universities. The tremendous decisive contributions of scientists in the present world conflict have popularly magnified science to its advantage and to its disadvantage. Apparently the final decision in this struggle will depend on superior arms and other equipment more than on greater manpower. The chief task of the sciences still

is to help provide as rapidly as possible the most effective means of destruction and the best care of our manpower. Especially through medicine, agriculture, engineering and industry, this is of course being done.

But in the coming aftermath, what may science, especially biological science, contribute toward the even greater task of rebuilding our devastated world and of reestablishing our profoundly disrupted civilization? It is inspiring to contemplate the prospects of a greater abundance of proper food, more widely, equitably distributed; of improved living conditions, improved health and a longer and happier life; of a better quality and perhaps a limited rate of reproduction. These and other advancements are not impossible, and some of these seem fairly assured. But our biological contributions need not, of course, end there.

Indeed, it may here be urged that, along with these splendid prospects toward helping to rebuild and improve this essential superstructure of our civilization, we should surely bear in mind, and help to clarify better in the public mind, the deeper foundation on which that superstructure rests. Otherwise, some of the very factors that enter into the rebuilding of our superstructure may sooner or later again contribute to its disruption.

The identity of that deeper foundation is in last analysis the essential nature of man, whose stability or instability must, in turn, determine the stability or instability of any superstructure built upon it. The conventional view that human nature, stable or not, can not be changed, seems not to have taken into account that human nature unknown may not be the equivalent of human nature known and understood. And we should likely further agree that one of the truly great contributions of our science has been the discovery and elucidation of the biological nature of man, or, for purposes of this discussion, of the relatedness of biological nature and human nature. We should, it seems, regard it a momentous step forward, a turning-point in mankind's study of man, when interest

and research came to be focussed less on the nature of things individually and more on things relatedly—when studies on man and the nature of man turned to studies on the related nature of things, including man.

Realization of this related nature of things had to await the discoveries of their common denominators. Such discoveries were indeed a triumph for scientific method and procedure. Where unaided experience had to stop, the scientist was not content to stop. By devising and improving special means to enhance his perceptions of nature, the scientist came to discover unity in nature where only diversity formerly appeared. This discovery of unity, of common denominators and the true relationships of natural phenomena might well merit greater emphasis these days, especially in the interest of a better-informed public. For it may here be agreed that recognition of this unity and corresponding relationships may properly demarcate the modern world from the ancient world. Knowing no common denominators, the ancients saw and emphasized differences in nature's manifestations and so, unable to understand or to control these diversities, they imposed in their gods and goddesses that understanding and control, thereby trying to satisfy their own ignorance and impotence.

These things certainly the public mind may come to know and duly appreciate. Accordingly, a better-informed public may also appreciate that the vast and rapidly advancing knowledge of inanimate and animate nature, which is literally transforming our modern world, owes its strides of progress largely to investigators who, more often than not, were least concerned about the immediate utility of their findings. Instead, their concern was and is better to understand the related nature of things, the beginnings of which obviously go back to the discoveries of units of matter and energy in things inanimate and of units of structure and functions in living things.

Yet how well we realize the present inadequacy of that

basic knowledge and how indispensably it must continue to advance, always beyond present frontiers, if human progress is to be maintained. The wide gap that so long has separated inanimate and animate nature assuredly, if slowly, is being closed. The laws of the physical world evidently obtain also in the living world. Properties of the physical basis of life are comparable with properties of other physical systems. The chemical nature of living things from bacteria to man, such as their similar nutrient requirements and enzyme systems, have their simpler counterparts in inanimate catalytic systems.

Thus it would seem that the picture of this related nature of things that is gradually being fashioned may be likened to a mighty spectrum, comprising both inanimate and animate nature, many of the lines of which are still poorly defined, but the existence of which can scarcely be questioned. The lines of that spectrum, however, would represent degrees or levels of organization, from the highest to the lowest in the living world, and downward without break into and throughout the physical world. In like manner, may not the uppermost limits of that so-called spectrum also link biological nature with the essential nature of man? If so, then may not human problems come to be more and more resolvable to biological problems? Hence, a biological approach to human problems is potentially something more than a figurative expression. Its validity inheres in a clear recognition of the biological relatedness of all living things.

Biologists, of course, clearly enough recognize that relatedness, and it is here suggested that it may be better clarified in the public mind. To that end, we are well aware that our science comprises a body of well-established general fact, as well as a reliable method by means of which that body of general fact was established, and by means of which also it is demonstrably true for all, including no less the informed public.

What that body of general fact is, certainly none of us here needs to be reminded. It constitutes the generaliza-

tions, the very essentials of our science. Indeed, it unifies our biological sciences into one science. Its generalizations were derived inductively and from them we may reason deductively. These represent the landmarks of progress in biological research and they serve as the guideposts in our elementary instruction. They are, so to speak, the A.B.C.'s of our science, and so in our various specializations they come to be largely taken for granted and perhaps may be unduly neglected. For purposes of this discussion, however, we may particularly note here that some of our most familiar, classical generalizations may most simply and strikingly disclose the essential relatedness of biological and human nature, notably in the interests of a better-informed public.

You will bear with me, therefore, if in briefly recalling this relatedness, I should cite certain of these generalizations that are familiar to every one here, only to point out some of their implications which are also obvious to us but which, it is urged, might well be made more clear and significant to the public. Accordingly I have chosen three classical generalizations that have to do mainly with structural, developmental and functional relatedness among living things, with special reference, of course, to man.

It was during this decade just one hundred years ago that biologists were greatly exercised over the then recent pronouncement of the cell theory. Similarities in the cells of plant and animal tissues were coming to be generally recognized and the viscid contents of cells were being explored. We realize more and more that the importance of those early investigations can scarcely be overestimated. But the point of emphasis for present purposes is that the extension of that theory came to include all living things—plants, animals, microorganisms and man. And so we can say, and the generations to come can say, that the living world is a cellular world, much as the inanimate world is molecular. And we now know that this protoplasmic unit is the unit not only of

the structure of living things, but also of their functions, their development, their heredity and their evolution.

Thus all living things, including man himself, in spite of their manifold diversity, have the same unit structure, perform the same elementary functions, begin their individual existence each from a relatively simple, primordial cell, transmit their hereditary factors by means of the same mechanisms, and from the mass upon mass of evidence, all things that live show these unmistakable marks of common relationship by virtue of a common origin.

And it is because of this common relationship that biologists can investigate monkeys or birds or frogs, fish, insects, flowering plants, marine plants, protozoa, bacteria or other organisms, and, if persistently, critically, deeply enough studied, they may come to find there, as others previously have found, not only phenomena that hold true for each of these organisms, or others of their kind, but eventually also some factor that is common to many or all of these and common no less to man himself. Modern studies on the relatedness of gene action and enzyme metabolism strikingly illustrate this.

But organisms are more than a mass of protoplasm or a group of cells; certainly more than only interacting atoms and molecules. Organisms have a history, a developmental, evolutionary history, which comprises both their ontogeny and their phylogeny. This salient fact, perhaps more than any other, distinguishes animate from inanimate nature. And this fact, we all might agree, needs to be taken into account in understanding the relatedness of biological and human nature.

For purposes of this discussion, a few diagrams of the well-known developmental series of animals, including man, are shown here by lantern slide. These diagrams are sufficient to recall that typically each organism, from protozoa to chordates, begins its individual life as an undifferentiated unit of protoplasm, a so-called primordial cell. Thus each living thing takes off at the same level, so to speak, at the primordial cell level. And, as

serially arranged, all proceed successively toward correspondingly higher levels of development along a similar course, each to its characteristic, fully differentiated, adult level (Fig. 1).

Divergencies in the courses thus followed are conspicuous and are important, of course, in other connections. But for present purposes, what matters most is the final level at which each line of development ends. The protozoan, beginning as an undifferentiated cell, ends as a

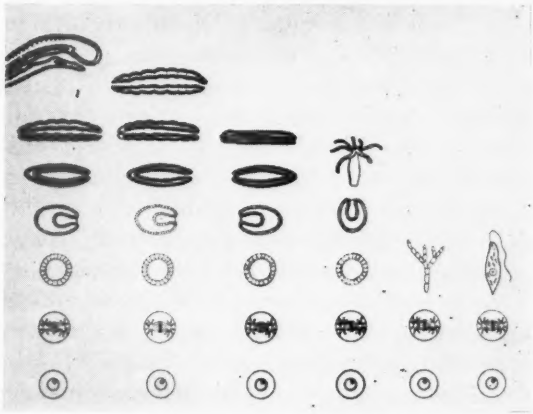

FIG. 1.

single differentiated cell. The coelenterate attains in its ontogeny the gastrula level, but remains essentially a differentiated, gastrula organism. And the successive levels of the flatworm with its third germ layer, of the round worm with its primitive coelome, and of the annelid with its added metamerism and its more highly differentiated organs and organ systems, are all familiar, classical examples. Finally, as also so well known here, the chordate reaches and exceeds all the preceding developmental levels, to attain among mammals, in the epigenetic differentiation of its neural tube, a mammalian brain, a primate brain and lastly the highly differentiated brain of man.

If now, allowing for many important omissions, we can

observe this degree of similarity to obtain throughout the entire gamut of animal organisms, from protozoa to man, what comparatively can we say regarding the degree of similarity among the members of a single species? Evidently the degree of similarity greatly outweighs the degree of difference. The former, indeed, is the basis for understanding the latter. And would it not appear that too much can be made and likely has been made of the degree of difference between groups of organisms in general, including, for example, the so-called races of men, and so not sufficient emphasis has been given to their degree of similarity? That organisms and groups of organisms differ and that races of men differ is hardly the question. Their variations obviously are always within limits. Is it not, then, the degree of difference that mainly matters? How to determine this and how to account for it remains a major biological problem, indeed many major problems which, especially from genetic evidence, appear now to have been partly solved. But in our efforts to identify and account for differences among men and other organisms, have we not unduly neglected their even more remarkable similarities? It is the latter, of course, that betrays their kinship, their common origin. And evidently it is this kinship, this degree of likeness, especially within our human species, that the public mind may well afford better to know and understand in the coming aftermath.

A further implication which this developmental series makes clear is the extraordinary stability that protoplasm has had evidently throughout the eons of evolutionary history. This, of course, accounts for the degree of similarity among organisms and it merits further brief consideration here in relating biological and human nature. Apparently phylogenetic history has also been essentially epigenetic in character. Each level of development in phylogeny, much as in ontogeny, was built upon preceding levels, always with various modifications, certain abridgements and consequent elisions. This pro-

cedure surely obtains no less for the evolutionary history of man. At least the main steps in that history seem to be unmistakable. These main steps have been modified and abridged but, as such, man incorporates them all.

In this sense, then, we may rightly regard human nature as essentially an extension of biological nature. Hence, we bear in our bodily form, and in our elementary functions, and in our reproduction and our heredity certain fundamental characteristics, certain tendencies and demands and desires which have clearly their more primitive counterpart in lower forms of life.

It is now a commonplace to say that man's unique place in nature can be attributed chiefly to the extraordinary superior development of his central nervous system, by means of which not only can he envision a better, healthier, happier civilization than he has ever known but also, it may be, he can thereby determine the means toward gradually realizing that kind of a civilization.

Working toward the fulfilment of that prospect, however, surely man has to bear in mind also that he, like lower forms of life, has a digestive system which demands food and will have food, even eventually at the cost of a deadly and destructive war. The significance of this well-known fact, especially for the public mind to recognize, is that that sort of insatiable, ravenous demand for food recurs in organisms without a central nervous system as well as in organisms having a central nervous system. Evidently, therefore, there is nothing essentially rational about hunger, and it may not be beyond our understanding if the more primitive, nutritive demands of man should at times exceed the bounds of his rational behavior.

In a similar sense, man, like lower forms of life, has differentiated a reproductive system whose natural demands for the procreation of his kind evidently had their origin not with the origin of man, nor with the origin of a central nervous system, but that origin of reproductive demands must have had its inception with the very origin

of life itself, for that is one of the fundamental, most primitive, universal characteristics of living things. Is it not probable, therefore, that the surges and upwellings in nature's demands to reproduce have their source for man much deeper than his rational self?

These few familiar examples of the truly profound relatedness of biological and human nature seem to urge that mankind's further study of man, in trying to solve man's individual and social problems, should seek better to ascertain the nature and limitations and degree of stability of his rational behavior as conditioned by his deeper, more primitive, non-rational functions. Since nutritive and reproductive functions, in both their developmental and evolutionary history, are more primitive than neural functions, is it not apparent that their role in conditioned behavior needs also to be duly recognized and well understood? May not such propensities as self and race preservation, common to man and lower organisms and now predominant in our recurring world conflict, spring from depths of our nature of which we are ordinarily unaware? Accordingly, could it be that both our defensive and offensive reactions are deeply rooted in the more primitive, nutritive and reproductive functions, well below our rational functions?

Such considerations serve to remind us that the essential problems of human progress are more than national or international problems. Among us, as naturalists, it may here be agreed that they are, first of all, problems of the human species, of the biological nature of man.

Our discussion thus far has been directed mainly toward's man past, his evolutionary past, as the basis for understanding his essential nature. But man is potentially more than the product of his past. He has aspirations, purposes, ideals which, so it would seem, may be regarded as essentially the more rational extensions of his formerly less rational and non-rational past. His further evolution, *i.e.*, his future progress toward fulfilling his now more rational purposes and ideals, evidently

must depend more and more upon his evolving knowledge and understanding. Knowing approximately the laws of nature and the evolution of his own nature, man may now not only look back upon the long and perilous road he has traveled, but, like the mythical Janus, man may also look forward with assurances, such as he in his blind past could never have, to a new and improving world which must increasingly be the product of his own rational creation.

The gradual realization of that kind of an increasingly rational progress would undoubtedly presuppose the continuous, unlimited advancement and diffusion of science, in the broadest and best sense of that term. To that end, then, is it not also apparent that the essential knowledge, the methods and the aims of our science will need to be better, more accurately clarified in the public mind, by improved means both within and outside our educational institutions? For it is the public who, sharing the benefits of human progress, must also share its responsibilities. And among those responsibilities obviously must be not only an intelligent support of science but also the protection of scientific progress, against any one or any group who would divert its proper course or misuse its results to thwart human progress anywhere. Such protection would thus constitute a kind of rear-guard protection of human progress, the vanguard of which will assuredly prove itself to be the unhampered progress of science.

# PLANTS AND THE MATERIAL BASIS OF CIVILIZATION

PROFESSOR EDMUND W. SINNOTT
YALE UNIVERSITY

WHETHER in recent centuries our civilization has really been making progress, or whether, as some insist, we are slowly spiralling downward to barbarism again is a question which historians and humanists and the lapse of time must ultimately decide. But in one aspect of man's life to-day—in his control over matter and energy—he surely has advanced far beyond the levels of the past and still goes forward with no sign of halting. The machine, with all the wealth of goods and services which it has placed at man's command, undeniably represents progress of a sort. We may well doubt its relevancy to those qualities by which the true ascent of man should be measured, and we may question whether his moral stature has yet reached a height where he can be trusted with so much physical power. Here it is that the advance of science touches these human problems so intimately, for the machine, with all it promises both of good and ill, is but an application of that vast fund of knowledge about the universe achieved by chemistry and physics since the eighteenth century. Our society, in a material sense, is built on the physical sciences.

We are less obviously dependent upon biology, though in all these years the biologists were not idle. Since the days of Linnaeus notable advances have been made in our knowledge of plants and animals. A recognition of the significance of protoplasm, of cellular organization, of the mechanism of heredity, of microorganisms, and of the character of metabolic processes generally are a few of the steps in its progress. Despite all this, biology has had a relatively small share in the rapid development of the material basis of civilization. To be sure, our greater knowledge of microorganisms has been of enormous value

in the prevention and control of disease, and better understanding of physiology has made of us a healthier and more efficient race. All this is immeasurably significant for the life of man, but of the material things on which this life depends, biology has given him much less than have the physical sciences.

Agriculture, of course, is still the foundation of society, and is concerned with the exploitation of plants and animals for man's benefit; but while applications of the physical sciences have completely changed the face of industry, those of botany and zoology have had much less effect upon agriculture. A farmer from the days of Virgil's "Georgics" would feel at home on an Italian farm to-day, but a craftsman of his time would be quite bewildered in a factory. Much of the increase in productiveness of agriculture in the past three generations has been due to its mechanization rather than to changes in its biological basis. I do not wish to undervalue the contributions of biology here which in the aggregate are very considerable, as in the development of superior animals and plants, in the discovery of more efficient methods of culture, in soil improvement and in other ways; but it is evident that these have been small in comparison to the contributions of the physical sciences to industry.

Such a result is not surprising. The material with which biologists deal is of extraordinary complexity, and much of their efforts thus far have been spent in preliminary reconnaissance. They have had to wait for discoveries to be made in the simpler domains of physics and chemistry before they could apply them to a study of living things. But in recent years the progress of biologists has become accelerated. Working in cooperation with biochemists, biophysicists and other fellow scientists, they have begun to gain a much more fundamental knowledge of the complexities of protoplasm and the organisms which it builds. These organisms are physicochemical machines, at many points intricate beyond our present powers to analyze but nevertheless machines and

subject to the same laws which have been found to operate in simpler mechanisms. They possess remarkable capacities for the synthesis of hosts of substances of great value to us, they run by power freely available in immense amounts, and they have an important advantage in that they do not need to be constructed by human effort and artifice but build themselves and even make provision for an ample succession of similar mechanisms. The time has come when our knowledge of these extraordinary living machines will make it possible to use them much more commonly and with far greater efficiency than at present. This employment may well lead to changes in our society so great that they will be comparable to those which followed the industrial revolution itself. Doubtless biology can minister to our time in loftier ways than these, and we never should lose sight of such a vital service. I propose to limit myself here, however, to the purely material level of our civilization and to discuss certain of the possibilities for its enrichment which may grow from the wider use of plants in the service of mankind.

Plants have almost a monopoly on the synthesis of those materials which are of primary importance to life. They hold, so to speak, the basic patents of the organic world. The synthesis of carbohydrates, amino acids and vitamins belongs almost entirely to them, and in their cells are manufactured a host of specific substances which are, or might be, of utmost usefulness. As "the groves were man's first temples," so were they his first chemical laboratories, but laboratories which he could neither understand nor enter. From them he extracted only a few of the more obvious products. It is toward a more complete utilization of the services offered by these remarkable synthesizing mechanisms that man's efforts are now turning.

Most familiar of these services is the production of food. Bread is the staff of life, and carbohydrates have always been the chief source of fuel for the human body. They are the immediate product of the most spectacular

synthetic process in plants, photosynthesis. The basic facts about this have long been known, but in recent years many of the details are being filled in. We know that both "light" and "dark" reactions are involved and that they differ in length; that, as shown by "tagged" atoms, it is the oxygen from the water, not from the carbon dioxide, which helps form the carbohydrate molecule; that many specific genes are involved in the development of chlorophyll; that a minimum number of light quanta is concerned for each molecule of product; that photosynthesis and the synthetic activities of some of the bacteria are similar in involving the transfer of combined hydrogen from a donor, such as water or hydrogen sulfide; and even that carbon dioxide may sometimes be built into carbon compounds in protoplasm without the agencies of light or chlorophyll. Such knowledge, if still further enriched and extended, should give us an intimate understanding of how light energy is trapped in the carbohydrate molecule by chlorophyll. This we can not yet repeat in the laboratory; nor if we could would we be able to compete with the cheap labor of sun and soil and leaf which it is the farmer's business to manipulate. But the process in most plants is inefficiently accomplished, and our greater knowledge will surely enable us so to improve these living machines, and to utilize their capacities so completely that an abundance of food may be within the reach of all mankind. Despite all that has been done to this end, much of the world is still hungry; and the spectre of catastrophe which Malthus raised, though pushed aside for a few generations, has never been laid. Agriculture, without a revision of its resources and methods in the light of our new knowledge of plant syntheses, will hardly be able to feed abundantly a much more densely populated world.

The problem of protein foods, those necessary tissue builders without which the physical basis of life itself can not be constructed, is even more difficult. Here, again, plants hold the basic patents, for they alone can

bring together carbohydrates and inorganic compounds of nitrogen to form the essential amino acids out of which all proteins must be built. Much more restricted is the invaluable capacity to tap the vast supply of nitrogen in the atmosphere, for this is possible to only a few bacteria; and the most notable among these, the root-tubercle bacteria, are almost confined, in their associations, to one plant family. The nitrogen available to other plants is limited chiefly to ammonium and nitrate compounds. The synthesis in plant tissues of the amino acids, upon which we ultimately depend for all our proteins, is thus subject to many restrictions, with the consequence that the production of a sufficient supply of protein foods becomes the most difficult problem in the nutrition of mankind.

Clearly one of the major tasks for those who would improve the service which plants give to man is to learn more about the manner in which protoplasm builds these compounds which form the physical basis of all life. A modest beginning has already been made toward this end. Amino acid synthesis is not as dramatic a process as photosynthesis, nor so easily recognized. It evidently is not the monopoly of any one organ, however, nor does it need light, for pieces of various tissues, isolated and in the dark, grown by the techniques of tissue culture and provided with sugar and mineral salts, produce protein abundantly. Synthesis seems to take place wherever new protoplasm is being formed, and is perhaps a part of the fundamental assimilatory capacity of all living matter. There are only a score or so of the amino acids, and they are formed through the mediation of enzymes by attachment of one or more ammonium radicles to specific organic acids. How this synthesis is brought about we do not know, but here, again, the "tagging" of atoms by use of radioactive isotopes or "heavy" carbon offers a hopeful method of attack. Plants differ markedly in their ability to synthesize particular amino acids, and these differences can be shown most easily and pre-

cisely in bacteria, yeasts, molds and other fungi, plants which have recently contributed much to our knowledge of physiology. In some of these organisms it is now possible to relate particular genetic changes to changes in the character of their amino-acid synthesis.

Practical results are already following studies of the protein metabolism of these lowly plants. One of the most spectacular of recent contributions to nutrition was the discovery that a strain of the yeast species *Torula utilis* is extraordinarily efficient in converting inorganic compounds of nitrogen into protein. This ability is already being utilized on a large scale to produce from the wastes of breweries and distilleries a supply of protein feed for livestock. Plans have also been worked out for the production of proteins for man by yeast, from cheap molasses and ammonia in the West Indies. Indeed, the remarkable versatility of yeasts in the synthesis of a host of useful compounds has led to the present intensive study of the physiology and genetics of these simple plants, which may well find a high place among the living mechanisms which can aid mankind. The yeast which our fathers prized for its mysterious services to bread and beer is a far more potent agent than they ever dreamed.

The nitrogen-fixing bacteria offer further hopeful material. Their secret has not yet been discovered nor the range of their plant associates widened, but enough has been learned of their physiology and of the differences which exist among them to warrant the hope that these differences may be increased to the point where such organisms may attach themselves to other plants than the Leguminosae. Meanwhile, the advantages which these bacteria confer upon this family have given its members a particular significance for man. The soybean, for example, has become a staple of our economy, producing almost everything from vitamins to doorknobs. The proteins made by some of its strains are very similar to those of meat. Protagonists of yeasts and of soys vie

with each other as to which can provide the most deceptive and nutritious imitations of T-bone steaks and pâté de foies gras, and vegetable "meats" of many sorts will one day appear on our tables. This does not mean that steers and hogs and capons will no longer form an important part of our diet, but it does show the immense resources, in protein foods of all sorts, which the plant kingdom can provide, and in a form much more direct and economical than from most animals.

Another hopeful method of gaining an abundant supply of proteins is a modern extension of a very old one—the use of the sea. Here untold myriads of minute plants take the abundant inorganic compounds of nitrogen formed from the decay of marine life or coming as outwash from the land, and build them into proteins. These plants, or organisms which feed upon them, ultimately form the food of fish, lobsters, shell-fish and other animals valuable in the nutrition of man and his livestock. It has recently been reported that a man's labor in the California sardine industry will yield several times as much protein as it does in the raising of beef cattle. The careful studies now being made of the sea and its inhabitants show how enormous is the potential supply of protein from this source and how much more fully the synthetic ability of these marine plants might be utilized in the service of man.

Equally important with energy foods and proteins are the vitamins. I need hardly discuss these, for they have become a matter of common knowledge and their name a household word. These substances, too, are produced almost exclusively by plants. The A vitamins are derived entirely from carotenoids, yellow pigments so frequently associated with chlorophyll in green plants. Vitamin C, ascorbic acid, is abundantly produced in plants, which are its source for man. The water-soluble or B vitamins, a notable series of substances, are entirely of plant origin. The unexpected fact has been established that several of these are as essential to plants as

they are to animals. Differences in the ability of plants, notably among the lower fungi, to make these vitamins has led to important information with regard to their synthesis. The profound effects of nutrition and other environmental factors upon vitamin production have been explored. Even their genetic basis has been analyzed and the ability to synthesize a specific vitamin has been related to a single gene mutation.

Beyond all this, the essential relation between vitamins and the complex enzyme systems operative in the respiratory processes of both animals and plants have now been established, and provide some of the most intimate glimpses yet gained into the metabolic activities of protoplasm. Studies of vitamin physiology have therefore proven important not only for their original purpose in human nutrition but in the more fundamental task of analyzing the biochemical behavior of protoplasm itself and thus helping to establish the basis for a more efficient employment of protoplasmic mechanisms in man's service.

This better understanding of the nature and synthetic ability of living plant machines will greatly aid in gaining an abundance of these various foods for man; but in other ways, as well, it should also be of utmost service to him. A host of plant products—woods, fibers, rubber, oils, drugs, dyes and many others—are familiar products of plant synthesis and we are far from exhausting their possibilities. The present intensive search for new sources of rubber, quinine, fibers and other materials now urgently needed has shown how numerous are the useful plants not hitherto recognized as such. The efforts of explorers, breeders and physiologists are continually adding to their number and efficiency. Most spectacular, perhaps, in recent days have again been the lower plants, with their production not only of proteins and vitamins but of those wonders of healing, the antibiotics, with penicillin at their head. Economic botany in the broad sense is still in its infancy.

But here an ambitious chemist may interrupt me to point out that many of these useful materials can be synthesized in the laboratory and that man can look forward to a day when he need be dependent no longer, for the myriad materials he needs, upon undirected synthesis in protoplasmic laboratories but can imitate and even improve upon their products in that house of marvels, the chemical laboratory. Ours is the age of chemistry. Chemurgy, the modern alchemy, devotes itself to just this synthesis of useful goods. It points to the manufacture of vitamins on a commercial scale; to the tremendous production of synthetic rubber, and to a multitude of other examples which are familiar to every one. But chemurgy goes much further than merely imitating plant products. It has provided us with scores of new ones. Synthetic fibers have revolutionized the textile industry. The use of plastics for almost every purpose leads some already to speak of the post-war world as the age of plastics. Synthetic drugs, like the sulfa group, have opened up new possibilities of healing. Give a chemist alcohol or cellulose or petroleum and he can make almost anything under the sun! What wonder that enthusiastic chemurgists believe our society will be made over by their art; that self-sufficiency will replace impoverishment for "have-not" peoples, and that international trade will no longer be concerned with raw materials.

But welcome as are the tremendous possibilities of chemistry for man's service, we should not forget two fundamental advantages which syntheses in plants have over those in the laboratory, advantages which will keep the material basis of our civilization still anchored firmly on the vegetable kingdom.

First, even with these plant products which can be made synthetically, this is in many cases uneconomical. Plants have, so to speak, such cheap power, raw materials and labor that they can defy competition from industries less fortunately situated, so that for most plant products there seems little likelihood of replacement by synthetic

substitutes. Indeed, chemical treatment of such products often so enhances their usefulness as to result in a much greater demand for them. Perfection of methods of wood treatment by which satisfactory pulp can be made from a wider variety of species than before, and of other techniques which produce much improved modifications such as plywood, plastic wood and impregnated wood, have enormously increased the usefulness of wood in our civilization, and made it of critical importance in the war. Not many years ago wood was regarded as a primitive sort of material, destined to be superseded by products better adapted to our mechanized society, and its return to a place of major importance is indicative of what may happen to other plant products.

Second, and more important, even where entirely new poducts are made, like rayon and the plastics, these must use as raw materials either the basic carbohydrates or a modification of them. Plants alone can unite carbon dioxide and water, and add nitrogen to them. These feats the cleverest chemist has not yet duplicated nor is he likely to do so, at least on a commercial scale. He must always come back to green plants.

The greatly increased demand for these basic products of plant synthesis, however, makes the growth of chemurgy highly significant to students of plant production. They must evidently devote their efforts less to the employment of plants for the synthesis of highly specialized materials and more for the mass production of raw stuffs needed by the chemist. Emphasis must be placed more on quantity than on quality. New plant sources must be explored. Surely it should not be necessary to use the grain harvest from 10,000,000 acres and much of the sugar crop, as we are now doing, to produce industrial alcohol. The demand for this material, especially acute now from its use in the making of rubber and explosives, will doubtless continue high during peace time because of the growing use of alcohol in industry. Here lies a great future for making alcohol from sawdust and other

wood wastes, on which such a hopeful beginning has already been made. The Scholler process, for example, is said to yield fifty gallons of alcohol from a ton of wood waste.[1] Here again, forests with their greater yield of plant material per acre per year, take on increased importance. More attention will also be given to the development of agricultural crops especially adapted to the requirements of industrial synthesis. The great increase in those chemical techniques which are certain to yield such a large part of the materials needed by the society of the future therefore does not mean that we shall depend less on plants but rather that we shall use their synthetic capacity even more, though often in different ways. Agriculture will continue to be the primary profession of mankind.

In addition to food and industrial materials there is a third way in which plants seem destined to contribute mightily to the material basis of our civilization. Society to-day rests upon machine industry, and machines need power. Coal and oil, the great sources of power, are reservoirs of the energy-rich products of photosynthesis in ages past. How long our supply of these invaluable materials will last is a much debated question. Some authorities say a shortage will begin to be felt in a decade or two; others that we need not worry for a few centuries more. However this may be, one fact is clear—this source of power is limited in amount and is being used up at an ever-increasing rate. War has shown how seriously a fuel shortage affects every aspect of our lives. Some day, assuredly, we shall have to get part or all of our power from other sources than organic matter in the earth's crust, and it is time that we began to explore their possibilities. Water power, wind, tides and atomic energy are either limited in amount or efficiency, or impossible to develop on a large scale. The direct fixation of solar energy by green plants in carbohydrate synthesis is still the most promising method of producing

[1] H. Harvey, *Science News Letter*, 45: 218–219, 1944.

materials which can be used as sources of power, and products of photosynthesis in living plants may before many years assume an importance in this respect equal to the products of this process in plants of past ages.

The total energy available from the sun is enormous—about $7.47 \times 10^{23}$ calories per year,[2] roughly equal to that liberated by the burning of 1,000 tons of coal over every acre of the earth's surface. Only a very small fraction of this is now fixed by green plants. It is estimated[3] that a field of vigorously growing corn plants uses in photosynthesis only about 1.6 per cent. of the light which falls upon it, and an acre of apple trees only 1.0 per cent. For the entire earth's surface, calculation shows that only .18 per cent. of the solar energy is fixed by plants.[2] Despite this inefficiency the total production of material is enormous. Some recent figures[2] indicate that land plants make about twenty billion tons of organic carbon per year. Another authority[4] estimates the amount as about thirty billion tons. Recent figures by him give the total world consumption of petroleum as the equivalent of 2,940,000,000 tons of carbon per year, so that the fixation of carbon by plants is equivalent to from six to ten times this amount.

These figures doubtless have a wide margin of error, but they agree in showing that the yearly amount of sun energy locked up in terrestrial plant materials is well in excess of the amount used to power our machines. Some of this product, of course, must be used as food for ourselves, our domestic animals and other living organisms. Some must be reserved for industrial purposes. Much would be lost in conversion to an available form. The remainder, theoretically available for fuel, is therefore probably not very greatly in excess of our fuel requirements. A well-planned economy should look forward to

[2] G. Riley, *American Scientist*, 32: 129–134, 1944. (References here to the papers of Noddack and Schroeder in this field.)

[3] E. N. Transeau, H. C. Sampson and L. H. Tiffany, "Textbook of Botany," p. 184. New York: Harper and Bros., 1940.

[4] E. Berl, *Science*, 99: 309–312, 1944.

means for increasing this photosynthetic product and making as much as possible of it available to man against the day when coal and oil grow scarce.

Several methods to this end suggest themselves. The most obvious is to increase agricultural production, almost all of which now goes for other purposes than fuel. Some increase can come from the development of more efficient crop plants, attainment of optimum growth conditions and elimination of losses from insects and fungi. More land can be brought under cultivation, especially in those wide areas of the tropics where conditions for plant growth are so favorable. More especially, crops can be grown which yield maximum amounts of plant material per acre, like sugar-cane and sweet potatoes, rather than many of our present staples.

A second line of attack is to secure a more complete utilization of the great body of plant products which now grow without cultivation, notably forest trees and other wild plants. Much more than half of the total terrestrial plant production is by forests, and per unit of area, annual production of organic material here is nearly half again as high as from cultivated land.[2] Forestry can doubtless increase this yield, and much could serve as fuel if efficient methods of conversion were developed. I have already mentioned the production of alcohol from sawdust. Another promising method has recently been proposed[4] for converting cellulose with relatively little energy loss into a product somewhat like petroleum. Not only wood can be used by this process but all cellulose wastes, which in the aggregate are very great, both in forests and on cultivated areas. These ordinarily decay, and by making them into fuel we should simply divert to our own uses the vast amount of energy now dissipated in the metabolism of the microorganisms which cause this decay.

A third source of power from plant syntheses, perhaps ultimately the most hopeful of all, is in the sea. Measurements of photosynthesis by algae of the marine plankton

is difficult, but recent estimates[2] indicate that the production of organic carbon by these plants is in the vicinity of 126 billion tons per year. This is more than six times the 20 billion tons already mentioned as a good estimate of production on land. It represents a yield of about 340 tons per square kilometer, more than twice the average of 160 tons for cultivated land. These are certainly noteworthy figures, for they show the tremendous photosynthetic capacity of marine plants. If we could tap effectively this enormous reserve, our worries as to carbohydrate production, whether for fuel or other purposes, would be over. Methods toward this end are hardly beyond the speculative stage, but it is clearly a major field of research for both the oceanographer and the botanist.

So through the years grows man's dependence on those living machines, the cells of plants. Despite perfection of mechanical techniques we shall evidently become more reliant, not less, upon the synthetic abilities of plants for the food we eat, the industrial products we require, and ultimately the fuel that shall power our mechanized civilization. The more extensive and efficient use of these protoplasmic mechanisms will require a much more intimate knowledge of their character and activities than we now possess. To provide this knowledge is the most urgent demand ever made upon the plant sciences, and places upon every botanist, and his collaborators in kindred fields, an important share in the responsibility for extending that command over nature upon which society depends. Protoplasm is the most intricate of mechanisms and its investigation is beset with endless difficulties, but very real progress has been made, and will continue, on many fronts. The unique capacity for photosynthesis, upon which rests so much of the significance of plants for man, must be explored more intensively. The establishment of the Kettering Foundation for work in this field is evidence of the importance which it holds in the eyes of enlightened industrialists. Similar studies must be extended into the equally notable ability of plants

to make simple nitrogenous compounds. The whole field of microbiology, which offers so many hopeful approaches to fundamental problems, must be carried far along the road it has so brilliantly opened. A study of all the so-called "growth substances," which has proven so stimulating to plant physiology and offers so many possibilities for practical application, must be carried much further. Other methods for the control of plant growth—hydroponics, vernalization, photoperiodism and more, unknown a few years ago—must be more widely extended. Genetics, which offers so much for plant improvement and has recently harnessed the tremendous stimulus of hybrid vigor in crop production, has many new paths to open, especially the fundamental problem of the mechanism of gene action in development. The plant explorer should by no means be forgotten, for surely there are hundreds of species, particularly in the wide tropical forests, which could be of great service to man. Those oceanographers who are opening up the tremendous domain of the life and activities of marine plants and animals may make a contribution beyond all the rest, and should be vigorously supported. Promising techniques of all sorts should be utilized. The beautiful method of exploring the inner recesses of metabolism by following the course of particular atoms which have been "tagged" by the use of radioactive or of "heavy" isotopes holds tremendous promise for us. Techniques for the sterile culture of bits of plant tissue opens many possibilities. Measurements of bioelectric potentials may give clues to be found in no other way. Indeed, whoever studies plants as living organisms and by whatever methods may make important contributions to the great problem which we face.

In an endeavor to improve plants for the service of man we should be encouraged by the fact, so often observed, that despite age-long evolutionary advances, plants are in many ways still notably limited and inefficient mechanisms, and that their possibilities for improvement are far greater than have ever been realized in nature. One of

our tasks is the stimulating one of directing their further evolution to our advantage and thus sharing, in small measure, in the great process of creation.

Difficulties in all these problems lie not in the absence of promising lines of attack but in the lack of men trained for the task. Well may we say that the harvest indeed is plenteous but the laborers are few. Laboratories supported by government, by industry and by our universities continue to multiply, but it becomes increasingly hard to staff them with properly qualified men. The great prestige of chemistry has in many cases persuaded administrators that chemical training alone is enough; but these protoplasmic mechanisms with which we work are of a different and more intricate sort than any machines of man's device, and the chemist is too often prone to a naive underestimation of their complexity. To investigate them successfully and to harness their powers to the service of man requires not only the arduous discipline of the physical sciences but a familiar acquaintance with that strange phenomenon which we call life. This difficult task must command fruitful collaboration from many sister sciences, but it is primarily the responsibility of plant biologists. To attract into this service a host of able students and to give them the broad yet thorough training which their profession demands will require from the leaders of the plant sciences a degree of vision and of statesmanship which transcends the narrow and technical view of this field which is held too often by the uninformed. The intensive employment of plants to provide an ever wider material basis for our civilization is one of the major tasks of our time, and here botanical science faces an opportunity for highest service to the life of man.

# REHABILITATION OF THE BIOLOGICAL SCIENCES IN THE POST-WAR PERIOD

PROFESSOR ROBERT CHAMBERS
NEW YORK UNIVERSITY

NEVER before has our organized civilization been brought face to face with such determining destinies, constructive and destructive, as are rampant to-day.

We all appreciate problems which confront us here at home. It is my purpose to show that concomitant with these are world problems vitally interrelated with ours. They have a common solution.

What is the scientist to do about this? Should he remain aloof from the social trends about him, believing that he can best serve by remaining in the seclusion of his laboratories? We know that, in his laboratory, he has developed a method with which he appraises his research, the scientific method, an objectivity of logical deductions based on observed facts. Is it not time that such objectivity be brought to the attention for use by our politicians and those who aspire to world making? But, in order that this scientific method be fully expressed, it is essential that scientific endeavor be free everywhere. Science takes no cognizance of national frontiers. Our best achievements require the sustained thinking of many minds in many countries. Hence, does it not appear that we, as scientists, can serve, not only as sponsors of the scientific method, but also as cooperators toward international unity?

Of immediate concern is Europe. In plans for the rehabilitation of her scientific and cultural institutions, there must be taken into account, not only the ravages of war, but also the building up of forces which are destructive to unity in science. Such debasing forces will have accomplished their aim, unless those who stand for the ideals of true science, take positive action in securing mutual cooperative fellowship, closer than ever before.

All agree that Europe must be free to work out her own salvation, but self-sufficiency in science is fictitious. A science tainted by a prejudicial attitude in one region of the earth will mislead many elsewhere. If we are to build up a healthy science here we must ensure intellectual freedom with opportunity and means for complete freedom of research, teaching and intercommunication everywhere. Science is a search for truth and she suffers if prostituted anywhere.

America will emerge from this war more important than ever before as a power in this world. Can we shirk our consequent responsibilities? The common man in Europe has long been impressed by America. To him America has been the haven of the oppressed and untainted with the evils of aggrandizement and imperialism. To us these values are worth many armies. Armies we shall have, and political power we shall have, but how much are we to implement these with intellectual and spiritual power?

One of the tragic consequences of war is the setback inflicted on progress in the basic sciences. On the other hand, a tremendous impetus has been given to the investigation of applying the bits of knowledge already acquired. This has, of necessity, disturbed the proper equilibrium between the basic and applied sciences. There has also been a shift of public interest and support to the application of the sciences rather than to the basic sciences which make the application possible!

Already, governments are beginning to consider ways and means of organizing scientific endeavor toward post-war security. In a recent message (*Nature,* editorial, 15/1/44) to the India Science Congress Association, Prime Minister Churchill said: "It is the great tragedy of our time that the fruits of science should, by a monstrous perversion, have been turned on so vast a scale, to evil ends. But that is no fault of science. Science has given to this generation the means of unlimited disaster or of unlimited progress. When this war is won we shall

have averted disaster. There will remain the greater task of directing knowledge lastingly towards the purposes of peace and human good. In this task the scientists of the world, united by the bond of a single purpose, which overtides all bounds of race and language, can play a leading and inspiring part." With reasonable effort the aspirations of this inspiring statement are bound to come true. But the issue must not be confused by restricting endeavor to utilitarianism. The application of science to industrial problems is popular. It won us the war. For this reason, Churchill's statement that "the task of directing knowledge lastingly toward the purposes of peace and good will" may be popularly misread unless the full significance of the term "lastingly" be realized. Then only can we hold that "science is pursued for the sake of knowledge of what eternally exists and not what comes for a moment into existence and then perishes." (Plato, Bk. III.)

Adequate provision must be made for the pursuit of knowledge for its own sake. We must strive to the end that scientific ideals be followed without hindrance and opportunities be open throughout the world. The solution of our economic, political and ethical problems requires the application to them of the scientific method. Out of this follows international cooperation, the value of which is twofold. It feeds science and accelerates it. It also is the most effective and, thus far, the least used tool we have for mutual understanding and good-will. Our active participation in the rehabilitation of post-war Europe presents an immediate challenge of implementing our aims toward scientific coordination in the post-war world which will be real and lasting.

The National Academy of Sciences and the National Research Council, both intended originally for wartime duties, have been eminently useful as permanent peacetime measures. The National Research Council possesses a Division of Foreign Relations which was initiated when the council was established in 1916. It is a member of

several international unions, of which one is the International Union of Biological Sciences. Many of its more active organizations deal with subjects such as geodesy, seismology, oceanography, which, by their nature, require continual international intercourse.

Of considerable interest is the contact of the National Research Council with the International Council of Scientific Unions which advises the League of Nations concerning scientific matters. In July, 1939, a meeting of the International Council of Scientific Unions took place in the Secretariat of the League of Nations at Geneva. In the Report of the National Academy of Sciences for 1939–1940 the plan proposed was presented as follows: "The plan was to consider the progress, interconnections and new directions of advance in the mechanical, physical, chemical and biological sciences with a view to promote the development of the scientific world picture. As a basis for this study, the countries adhering to the council were requested to contribute résumés of the status of scientific research in these several countries." The war put an end to further action which might have initiated a new èra in science!

In the Report of the National Academy of Sciences for 1942–3 the ruthlessness of the present war is deplored and, by contrast, an incident of 1813 is related which occurred "during the war between France and England when Sir Humphry Davy visited Paris and was awarded a gold medal of the Académie des Sciences, and elected corresponding member. Such amenities have long since vanished." But should we desire such amenities to persist? That was the time when war was regarded as a chivalrous pastime, a gentleman's profession! Since then, its masks have been successively ripped off and war stands out to-day in its stark reality of unmitigated brutality and wickedness. Shorn of every vestige of decency it can not long survive!

During the war period, attention has been largely devoted to Inter-American activities. The International

Union of Chemistry is organizing a Hemisphere Branch of the union for the purpose of "bringing together chemists of the American Republics. Students of chemistry are being welcomed and trained in the United States." In 1942 the governing board of the Pan-American Union set up an Inter-American Institute of Agricultural Sciences. This was supported by a grant-in-aid from the Coordinator of Inter-American affairs. The Division of Biology and Agriculture of the National Research Council had long advocated the establishment of such an institute. A project also has been started to provide scientists in the other American republics with copies in microfilm of scientific literature available in this country.

Somewhat further afield have been the activities of the American Astronomical Society which, with financial aid from the National Research Council, "has distributed to astronomers in Sweden, Finland, Great Britain, the Union of Soviet Socialist Republics, and Switzerland, information regarding advances in a monthly news letter. Further distribution through embassies and foreign astronomers has brought favorable comment from Australia, Argentina, Mexico, Turkey and other countries."

The Department of State is actively participating in the furtherance of international good-will. The activities of the Division of Cultural Cooperation, established in 1938, are presented in a 71-page pamphlet, "The Cultural Cooperation Program," 1938–43 (obtainable from the Superintendent of Documents, Government Printing Office, Washington, D. C.). During the period of 1938–41 the program was focussed on the Western Hemisphere. This has included travel and study grants; the exchange of professors and books; assistance to U. S. cultural centers, such as libraries, institutes and schools; and the distribution of informational motion pictures. In 1942 the scope of the program was enlarged to the extent of urging "a vigorous development of cultural relations between the people of the United States and other free peoples of the world, for the purpose of fostering helpful

international relations on a basis of mutual understanding and appreciation." The plan includes "interchanges in all fields of the arts, sciences, technology, letters and education, and throughout the entire ramp of economic and social life." "The interchanges should serve to promote human welfare and help to preserve intellectual and cultural freedom."

Encouraged by the scope of this program, a group at the Marine Biological Laboratory at Woods Hole invited a representative of the Department of State to address the scientific community at Woods Hole. Mr. G. Howland Shaw, Assistant Secretary of State, sent, as his representative, Dr. Ralph E. Turner. As a result of stimulating sessions with him a memorandum was prepared expressing the interest of the biologists in participating with the State Department in efforts toward rehabilitation of the basic biological sciences during the post-war period. Briefly stated, the memorandum recommends closer cooperation than hitherto among scientists throughout the world. The need for rehabilitation as a result of war devastation is presented as an opportunity for furthering such cooperation. Suggestions are offered (1) of increased support toward international scientific congresses taking into consideration the inestimable value of frequent personal contacts; (2) of the establishment of representatives of the basic sciences in governmental embassies to enhance close coordination of scientific investigations; (3) of prompt rehabilitation of scholars of the basic sciences with needed laboratory and library equipment; (4) of the establishment of short- and long-term exchange fellowships and professorships.

A memorandum, similar in scope, has been recently and independently prepared by Joseph Needham at the University of Cambridge and was sent to our National Research Council for consideration. It is entitled "Memorandum on an International Science Cooperation Service."

In the last published Report of the National Academy

of Sciences for 1942–43, the extent to which international matters have been considered, aside from those already referred to here, is shown by the following: In a conference held on August 7, 1942, between one of the secretaries of the Royal Society of London and the chairman of the Division of Foreign Relations, it was agreed that "after the war opportune cooperative understandings with learned societies of previously hostile nations might be a better way of restoring mutual friendship and respect than an attempt, now, on our part alone, to fix a definite policy of collaboration."

However, early in 1944 the Foreign Relations Committee of the National Research Council organized plans for a conference on "Problems of Restoring International Scientific and Scholarly Cooperation." The topics being considered are the exchange of scientific literature, restoration of libraries and resumption of international activities. Plans are also being prepared as to the means of obtaining information regarding needs of scientific workers, exchange of scientific personnel and the relation of present international scientific organizations to meet a United Nations' organization, as may be created. A notable feature of the program is enlisting the interest of the Department of State, with reference to assistance in participation of specific projects of research and publication, to congresses held in the United States and to attendance of Americans in international congresses in other countries.

It is stimulating to realize that the immediate need of post-war restoration is serving to institute, more intimately than hitherto, long-range cooperation among workers in the basic sciences of all freedom-loving countries throughout the world.

The preparation of such a project requires action on the part of every one interested. At least two steps should be taken: (1) contacts should be made to coordinate the activities of foreign and domestic relief committees, which are engaged in plans for the rehabilitation of edu-

cational facilities in the war-stricken countries. In such efforts notable assistance is already being given by the Rockefeller Foundation to foreign scientists and to scientific institutions abroad. The Royal Society of London is also engaged in similar activities. (2) By means of Needham's and the Woods Hole Memoranda, or a combination or revision of both, there should be secured at once the active collaboration of all interested individuals and institutions both in North and South America and in other freedom-loving countries overseas, which have been least affected by the material damages of the war.

Ideas emanate from the least expected places. The broader the source and the wider the range of proposed ideas, the more likely will be the chances of preparing a permanently working plan.

A comity of nations depends upon mutual respect for the differences which exist among them. There also exist threads of similarities, a chief one of which is the universal appreciation of science and the scientific method. This provides one of the surest approaches to mutual understanding and good-will.

# THE SPADEFOOT TOADS IN OKLAHOMA WITH A SUMMARY OF OUR KNOWLEDGE OF THE GROUP. II

DR. ARTHUR N. BRAGG
UNIVERSITY OF OKLAHOMA

## THE BREEDING PATTERNS OF SPADEFOOTS

Those who have studied at first hand the breeding habits of the frogs and toads of the moister regions of the country only have usually found that most of them manifest several tendencies in common, although of course differing specifically in details of behavior. One of these common tendencies is to have a rather definite season during which all breeding of any one species takes place. Another is the tendency for this breeding season to begin early in the spring (as in various hylids and the leopard frogs), although some (as the American toad in the East, and the bullfrog) wait till later. While most of these species may be stimulated by spring rainfall, almost none are dependent upon this for the initiation of breeding behavior and, with limited exceptions, none breed (either with or without more rainfall) after the breeding season has passed. Because of these trends, making up what I choose to call a breeding pattern, it has been widely assumed that all our frogs and toads have a breeding season, modified to some extent by rainfall and more by latitude (or factors limited by this).

My studies with the Oklahoma forms have convinced me that not all North American frogs and toads manifest the same breeding pattern (Bragg and Smith, 1942). In Oklahoma there are two principal patterns, one characteristic of those species especially adapted to drier habitats and manifested especially by those limited to the grasslands or other more xeric environments; the other shown by those organisms which inhabit moister environments (woodlands, savannahs, etc.), whether restricted to these habitats or not. The prairie-limited species, and

others living in woodlands as well as in the prairie, commonly do not have a breeding season at all except in so far as the whole period from early spring to early fall may be considered to be one. For convenience, I propose to call the breeding pattern characterized by a breeding season little influenced by rain the *mesic pattern,* that characterized by no breeding season with all breeding initiated by rainfall, the *xeric pattern.* All the eastern species of *Rana, Bufo* and Hylidae tend to have the mesic pattern. In Oklahoma, *Rana catesbeiana, R. a. areolata, R. a. circulosa, R. clamitans, Bufo a. americanus, B. woodhousii fowleri, Hyla v. versicolor* and *Pseudacris streckeri* are among those exhibiting the mesic pattern. On the other hand, *Bufo cognatus, B. compactilis, B. insidior, Pseudacris clarkii, Ps. triseriata, Microhyla olivacea* and all species of spadefoots have the xeric pattern. *B. woodhousii woodhousii* and the common leopard frog (somewhat doubtfully referred to *Rana sphenocephala* Cope in all my publications) are intermediate, both breeding early in the springtime regardless of rain but also breeding at any time to early fall with any considerable rains which fall. The tadpoles of the leopard frog have been found at Norman, Oklahoma, in January developing from eggs laid the previous fall.

As related to the spadefoot toads, the xeric pattern is most interesting; for nowhere else is it shown in so clear-cut and unequivocal manner. All species so far studied, regardless of their normal environment, are alike in the following: (1) *There is no definite breeding season.* Congresses of these animals may occur at any time from early spring to mid-September whenever conditions are right. Or, in any given area, spadefoots may not breed at all during a year (or several years) if conditions fail to be suitable during this time. Trowbridge and Trowbridge (1937) seemed to have evidence of a breeding season in *S. bombifrons,* but Bragg and Smith (1942) have shown that this was not the case. (2) *Spadefoots usually breed only during or after rains.* Only one exception is

known—Linsdale (1938) reported breeding activities of *S. hammondii* in Nevada when a mountain stream overflowed its banks in a dry area. (3) *Spadefoots breed only (or almost exclusively) in temporary water.* (4) *Spadefoots of both sexes are greatly stimulated by the calls of their own species and tend to migrate toward places where others are calling.* Hence, the usual spadefoot chorus in a given pool is a loud and very noisy one. (5) *All male spadefoots have loud, rather harsh voices with great carrying power.* A large chorus of *S. bombifrons, S. hammondii* or *S. couchii* can be heard for at least two miles on a still night and much farther when carried downwind. The call of the individual *S. hurterii* appears to be not so loud, but I have detected a chorus of not more than a dozen individuals from a measured distance of 1½ miles against a breeze and over two low hills in woodland. All who have reported on *S. h. holbrookii* describe its call as very loud and harsh. (6) *Spadefoot breeding is inhibited by low temperature,* but the exact conditions are unknown except for *S. bombifrons.* This form emerges to breed in numbers at an air temperature above about 11° C. (Bragg and Smith, 1942), although great stimulation by rainfall when in conflict with inhibition by cold varies this point slightly, so that a few males may call at and just below 9° C. Emergence of *S. h. holbrookii* was thought by Ball (1936) to be influenced by ground temperature. The conditions with *S. hurterii* are somewhat uncertain. In the spring of 1942, they did not enter known breeding pools and could not be found out feeding all through early April, after rains which made this the wettest April in central Oklahoma for many years and at temperatures varying between 9° and 15° C. But on April 24, a small breeding congress developed during a rain which totaled less than many which has occurred earlier and at lower temperatures. It is possible that an accumulation of rainfall, such as suggested by Trowbridge and Trowbridge (1937) for *S. bombifrons,* may be necessary for *S. hurterii* (and perhaps also for *S. h.*

*holbrookii*). Should this prove to be the case, then of course the temperatures observed in the spring of 1942 would have questionable significance. The effect of temperature on the breeding of *S. couchii* is apparently wholly unknown. It so happens that I have had opportunity to observe them only in late spring and summer when nothing could be learned about this. (7) *Spadefoot embryos and larvae have an intrinsically high developmental rate.* This has been shown particularly for *S. bombifrons* by Trowbridge and Trowbridge (1937) and by M. S. Trowbridge (1941). For *S. h. holbrookii* it has been mentioned by numerous investigators; for *S. couchii* by Ortenburger and Ortenburger (1936); for *S. hammondii* by Bragg (1941c) and for *S. hurterii* by Bragg (1943). (8) *Developmental rates vary greatly with temperature under otherwise comparable conditions.* Spadefoot tadpoles (at least of all the western species which I have studied) can withstand very much higher water temperatures (and greater fluctuations) than usual with Amphibia. I have found them living normally in prairie pools at water temperatures between 39° and 40° C.; temperatures, moreover, higher than those which have killed tadpoles of *Pseudacris streckeri* and *Bufo a. americanus* in other pools in the same region. Under these conditions, tadpoles of the same age within one pool have varied considerably in size although there is an interspecific difference in degree of such variation, especially in *S. hammondii* (Bragg, 1941c). (9) *The tendency of the tadpoles toward carnivorous habits and cannibalism is marked.*

The type of habit-patterns exhibited by spadefoots, irrespective of the ecological or geographic distribution now shown, suggests strongly adaptation to drier habitats than some of them now occupy. In fact, this alone is enough to indicate strongly an origin of the group in deserts or drier types of grassland from which some species have now spread to moister regions such as the eastern woodlands. This hypothesis is also in accord

with the fossorial and almost completely nocturnal habits of the adults and it will explain the marked difference in behavior of *S. h. holbrookii* from all other Salientia of the East, a fact which has always occasioned much interest and often no little surprise when first observed.

If we keep this idea in mind while we examine the interspecific or intergroup differences among species of *Scaphiopus,* further interesting interpretations emerge. The facts upon which these interpretations rest are as follows:

(1) In relation to breeding after rain, *S. h. holbrookii* and *S. hurterii* are greatly stimulated by large amounts of rainfall; not, apparently, so much by its rate of fall. Practically all accounts of the former species speak of the rain which stimulated the observed breeding congresses as *heavy* rather than as *violent* (see Ball, 1936). In regard to *S. hurterii,* it is of interest to note that I have watched the area in central Oklahoma where this species was first reported by Smith and Leonard (1934) for six consecutive years without once finding evidence of their breeding until the record-breaking rains of 1941 (Bragg, 1942). During that spring, however, several congresses developed both here and elsewhere in eastern Oklahoma and tadpoles went through metamorphosis (Bragg, 1943). But, in the spring of 1942, in the same area, these animals did not breed in numbers, although a few males called from one pool during a heavy rain one evening.

On the other hand, *S. bombifrons, S. hammondii* and *S. couchii* all may breed successfully after as little as one half inch of rain, provided its rate of fall is exceptionally fast. This has been most clearly demonstrated in *S. bombifrons* by Bragg and Smith (1942) who also show that this species does not always breed after non-violent rains of as much as two inches when all other conditions are favorable (see also Bragg, 1941c). It seems clear, therefore, that violence of storms is the important factor in this group of species whereas amount of rain is secondary, the exact reverse of conditions in the first-mentioned group. A very violent storm (whether also

heavy or not) may overcome some of the inhibition of low temperatures or the tendency toward completely nocturnal habits, in *S. bombifrons* at least, but there is no case on record, so far as I can find, of *S. h. holbrookii* or *S. hurterii* breeding in daylight.

(2) Breeding sites often seem to be selected differently among the various species. I am informed by Dr. A. I. Ortenburger (see Ortenburger, 1926) that in Arizona he observed *S. hammondii* in a small pool only about 100 yards from *S. couchii* in a larger one of a different type. He could not remember with certainty that there was no mixing of species, but he is sure that there was a very great preponderance of the one in the first pool and of the other in the second. Similarly, in New Mexico (Bragg, 1941c) I noted that some pools developed congresses of either *S. bombifrons* alone or *S. hammondii* alone, whereas others contained a mixture of the two. It is interesting to note that where individuals of both species were present, they seemed to be in approximately equal numbers. Only rarely did I find a pool mostly of the one with only a few of the other. Similarly, Dr. Charles C. Smith and I have noted in southwestern Oklahoma that *S. couchii* more often breeds in the same pools as *Bufo compactilis* than in those pools also containing *S. bombifrons,* although we have seen these spadefoot species together on several occasions. The evidence, so far as it goes, indicates that depth of water may be one factor in this situation, although we need more observations on this specific point. From several years' experience with an aggregate of several hundreds of breeding congresses I have a definite impression that *S. couchii, S. hammondii* and *S. hurterii* commonly breed in more shallow water than *S. bombifrons. S. multiplicatus* at least sometimes uses shallow water (Taylor, 1942) and *S. intermontanus* also uses shallow pools, even if the water be brackish (Tanner, 1939).

There are two complicating factors here, however, which must not be overlooked: (a) all spadefoots which I have observed manifest a marked tendency to use any

temporary water available and all those which usually are found in deep water may breed in shallow water if deep water is not present in the immediate vicinity; and (b) the observed segregation in pools may be only the result of what type of pool is found by the first emerging spadefoot of any one species because of the marked attraction to the calls of its own kind. These are undoubtedly factors in a complicated situation which only further experience can finally clear up.

(3) The tadpoles as well as adults of *Scaphiopus* are interesting in that they differ subgenerically in general size. Those of all species of Spea are larger and develop into at most medium-sized adults. On the other hand, those of subgenus Scaphiopus are much smaller but develop into larger adults. This is shown by summarizing lengths of adults and larvae as given in the literature cited and from my own measurements. Calculation shows that in all species of Spea the tadpoles are approximately as long in total length as the adults, whereas in Scaphiopus they are not nearly so long, either relatively or absolutely. Adults of Spea are about 55 mm in length, their tadpoles 59 (disregarding as unimportant to the point being made here the considerable variation among individuals). The same figures in Scaphiopus are 65 and 25, respectively. Furthermore, there is not nearly so much interspecific as subgeneric variation, as shown by the following approximate figures of length in mm of adults and larvae (adult figures given first): *bombifrons,* 55 and 65; *hammondii,* 53 and 68; *intermontanus,* 55 and 51; *multiplicatus,* 55 and 51; *h. holbrookii,* 61 and 28; *hurterii,* 65 and 23; *couchii,* 70 and 25.

(4) Another difference in tadpoles among certain species may or may not have significance. Those of *S. h. holbrookii* sometimes form schools in which there seem to be cannibalistic tendencies manifest (Ball, 1936). Those of *S. hurterii* also may form schools, but no cannibalism has been noted. In the latter case the phenomenon is clearly social in character as observed regularly in a single pool when the tadpoles approached metamorpho-

sis. (For details see Bragg, 1943.) So far as I can determine, such behavior has not been observed in any species in Spea.

(5) Behavior during and just after metamorphosis also varies among species. This has been noted specifically for *S. bombifrons* and *S. hurterii* in central Oklahoma. Since this difference in behavior appears to have a direct bearing upon ecological limitation of the geographic range of *S. hurterii,* it seems advisable to contrast the two briefly. Upon leaving the natal pool, a young individual of *S. bombifrons* seeks protection from desiccation by burrowing immediately into the mud near the water (see G. A. Moore, 1937). In very hot weather and bright sunshine this may occur even before the tail is much absorbed. For the next few days the young spadefoot remains in its burrow but may emerge at night, or after showers, to feed. It never allows itself to become dried out. Within a week or so the young animal wanders from the region of the pool, thereafter burrowing in any favorable spot each dawn after nights of feeding. From this time forward it exhibits essentially the habits of the adults.

In contrast, *S. hurterii* does not burrow immediately upon leaving the pool but seeks protection beneath leaves or other appropriate objects nearby. Even in very hot weather, the tiny animals refuse to enter the water again, once they are on the bank, and, if not shaded, will die by the thousands at the pool's edge, even on moist mud. Those that find protection beneath leaves rest there during the days immediately after metamorphosis but emerge at night to feed. In about one week, all suddenly disappear. I have not determined where they go. It seems likely that it is then that they begin burrowing but it may be only that they scatter widely after the manner of *Bufo a. americanus* in the same habitat. Thereafter they still emerge at night to feed and have been found rarely at this activity. From the first, however, they are more secretive than *S. bombifrons.*

The essential point is that *S. hurterii* could only under

quite exceptional conditions emerge from a prairie pool such as constitutes the typical breeding site of *S. bombifrons,* because of a difference in the stage of development in the two species at which the burrowing instinct first becomes expressed. From this it follows that one of the limiting factors (perhaps the principal one) which keeps *S. hurterii* a woodland form is the inability of its young to metamorphose successfully in a prairie under the usual conditions obtaining there. Details in other species are not known sufficiently to say positively how they may fit into this picture, although Cope's (1889) observations suggest that *hammondii* is essentially like *bombifrons* in this respect.

(6) There is still one more phase in the breeding of the spadefoots which must be mentioned. In *Bufo,* the studies of Bragg (1940, 1940a), Blair (1941, 1942) and Bragg and Smith (1942) have shown that interspecific differences in breeding patterns, in breeding season and in calls play a large part in sexual isolation; and Blair particularly has emphasized these as isolating mechanisms among some of the eastern toads. In the prairie species (*i.e.,* those confined to prairies) the difference in breeding season is no factor at all, since all these follow the rains in breeding rather than the seasons (Bragg, 1940, 1940a, 1940b, Bragg and Smith, 1942, 1943). Call, differential behavior of the sexes and various differences in detail of breeding behavior, including differentials in selection of breeding sites, are very important in sexual isolation of various closely related and probably interfertile species.

The spadefoot toads are generally like the prairie-species of *Bufo* in these respects and have essentially the same types of isolating mechanisms. These mechanisms may all be conveniently grouped as either (a) physiological (or psychological), (b) ecological, or (c) geographic (so obvious as to need no further mention).

Physiological factors among the spadefoots involve principally a differential response to calls and a different pattern of male behavior in securing mates. The first of

these has already been emphasized in other connections, but the second needs further elucidation.

The male of *Scaphiopus bombifrons* floats on the surface and calls repeatedly from one place without much moving about. Females are greatly attracted by this call, enter the pool and swim to the male, the latter paying little attention till touched by one of them, whereupon clasping occurs. The male of the closely related *S. hammondii* also calls from the surface; but in this case, the male swims about almost continuously while calling and rushes toward any other spadefoot in its vicinity attempting to clasp it (Ortenburger, 1925; Bragg, 1941c). If two males meet (and this is frequent) each struggles for position till one has attained it, but the clasped male is released immediately upon its croaking. Since females of *S. hammondii* also respond markedly to the call of the male, any female caught by a male is most likely to be of the same species. This difference in behavior appears to be the principal isolating mechanism between these two species when present together in the same pool. However, the possible segregation of species within adjacent pools under the influence of the voices of the first arrivals in each should not be overlooked.

*Scaphiopus couchii* and *S. hurterii* are similarly sexually isolated. The former most frequently calls on or near the banks of a pool, according to Ortenburger (1926), although it is not uncommon to find them calling while floating in the typical spadefoot manner. *S. hurterii* manifests the reverse tendencies, *i.e.,* whereas some may call from the bank (Smith and Leonard, 1934; Bragg, 1943) most matings appear to be at the surface of deeper water. As with *S. hammondii,* so with *S. hurterii* I have seen calling males rush at each other, struggle for the clasping position, and then separate immediately upon the croak of the unsuccessful member of the pair.

Since both sexes of *S. h. holbrookii* float at the surface and the male apparently awaits a female with little moving about (Ball, 1936), this species is probably sexually isolated from *S. hurterii* when breeding together (as is

possible in Arkansas and eastern Texas) by the same factors which separate *S. bombifrons* and *S. hammondii.*

Ecological isolation is only partial in the spadefoots and may be looked upon as merely accessory to the psychological factors emphasized above. *S. bombifrons* commonly is found only in deeper pools. At Las Vegas, New Mexico, in 1940, I was struck by the fact that every pool in which *S. hammondii* alone was calling, as well as every pool from which I later secured tadpoles of this species only, was shallow; whereas, all deeper pools examined contained tadpoles of *S. bombifrons* and no *S. hammondii.* Pools of intermediate depth contained both species. Nevertheless, the most shallow pool of all contained only *S. bombifrons,* as explained elsewhere (Bragg, 1941c). I have also since found *S. bombifrons* in Oklahoma calling from shallow water. As mentioned earlier, *S. couchii* commonly breeds in much more shallow pools than *S. bombifrons. S. hurterii* uses both shallow and deep water apparently indiscriminately, but *S. h. holbrookii* seems from the accounts which I have read to be most common in deeper pools.

Tanner's (1939) account of *S. intermontanus* suggests that this species is also indiscriminate as to the depth of water. He says, "Great numbers in copula were observed at a small playa. . . ." This seems to indicate shallow water. On the other hand his statement, "Tadpoles were collected in the Price City Reservoir . . ." may imply fairly deep water. Concerning *S. multiplacatus,* we have only the statement of Taylor (1942) made in reference to tadpoles: "The shallow pool where they were collected was formed in an excavation where the earth had been removed in road building."

Another factor (in part psychological, in part ecological and in part physiological) tends to eliminate possible interspecific breeding. This is the already mentioned tendency for some species to be influenced more by heavy rains, others more by violent rains. This, however, is a minor factor, since it tends to be associated with a particular environment and, hence, to work potentially be-

tween only those species which occupy different habitats and are not likely to occur in the same pool. It may become important in areas where ranges overlap as in northern Texas, where *S. couchii's* range overlaps that of *S. hurterii*, or in east central Oklahoma, where the latter form meets *S. bombifrons* geographically (but not ecologically). In the latter situation, a few *S. bombifrons* inhabiting prairie islands may move into pools in adjacent woodland or savannah where *S. hurterii* breeds. After violent (but not particularly heavy) rains, *S. bombifrons* may breed here in small numbers without *S. hurterii* being affected. When, however, rains are both violent and heavy, the two species breed together. If, however, prairie islands have temporary pools within them then these are utilized by *S. bombifrons* and only very seldom by *S. hurterii*. In this case, the segregation and sexual isolation are entirely due to ecological factors.

Disregarding geographic isolation as so obviously an isolating mechanism as to need no special comment, we may summarize the above discussion as follows: even though all species of *Scaphiopus* follow a generally similar pattern of breeding, they are quite effectively sexually isolated even when breeding in the same pools. While several interacting factors play their parts, the two principal ones are (1) differences in details of how males secure females and (2) the attraction of the calls of the males for females of the same species.

## Phylogenetic Interpretations

Those interested in speciation and other phases of organic evolution have quite naturally made most use of morphological variations in interpreting phylogenetic relationships and geographical distributions in groups with which they have happened to be dealing. Only rarely and quite recently have I noted much tendency to include habit-patterns in such interpretations except as quite incidental to the major morphological basis. Specifically within the anuran amphibians, taxonomists have based interpretations upon detailed measurements, color

factors, other external features, and (more rarely) detailed differences in internal anatomy (muscles, skeletons, type and arrangement of teeth, etc.). Zoogeographers have also utilized such characters in correlating these with distribution as found in attempting to arrive at reasonable conclusions as to the origin and dispersal of this or that family or genus. Another group of scientists, smaller in number but of some significance, have looked into the habits of individual species or groups, studied the tadpoles, and elucidated other phases of life histories. One of the foremost of these is Wright (1914, 1929, 1931, etc.).

While each of these groups of students has added valuable contributions to our general knowledge within their respective fields and while all workers have realized that habits must play an important part in the lives of organisms in nature, very seldom has an attempt at a synthesis of all of these factors been made in tracing phylogenies. Habits particularly, partly through lack of knowledge, have often been neglected. For this reason habits are emphasized here.

The spadefoot toads are generally supposed to have arisen in southwestern North America and to have spread geographically from there, differentiating into the various species as they dispersed. Tanner (1939) says, "Geographically, the subgenera are fairly distinct, having evolved, it would seem, from a common center of origin near northern Mexico, the subgenus Scaphiopus having radiated into eastern United States, while the subgenus Spea is found in the western United States." Tanner offers no opinion as to the phylogenetic line followed within the subgenus Scaphiopus but, concerning Spea, he says, "The evolution of the subgenus Spea seems to be from *hammondii* through *bombifrons* to *intermontanus*." This opinion was based principally upon a progressive change in the skeleton of the head but may have been influenced somewhat by the supposed closer resemblance of the mouth parts of the tadpoles of *inter-*

*montanus* to those of *hammondii* than to those of *bombifrons*. Actually, the *bombifrons* tadpole more closely resembles that of *intermontanus* than that of *hammondii* (see Bragg, 1941b) as also do those of *multiplicatus* as recently described by Taylor (1942). Of all the larvae within Spea, those of *hammondii* are the most distinctive. In some circles there is a tendency to emphasize embry-

TABLE I

Some characteristics of the subgenus Spea as contrasted with the subgenus Scaphiopus. Italics are used to show wherein *S. couchii* departs from its taxonomic relatives and is more like members of Spea. It will be noted that, so far as knowledge goes, this is always at points where habits rather than morphology are involved. (?) = no conclusive date for *couchii*:

| Spea (All in xeric habitats) | Scaphiopus (All, except *couchii*, in mesic habitats) |
|---|---|
| 1. Eggs large. | 1. Eggs small. |
| 2. Eggs light in color. | 2. Eggs dark in color. |
| 3. Adults small. | 3. Adults large. |
| 4. Tadpoles large. | 4. Tadpoles small. |
| 5. No tendency of schooling of tadpoles at metamorphosis. | 5. Tendency (under some conditions) to school at metamorphosis. (?) |
| 6. Young burrow immediately on leaving pool. | 6. Young delay burrowing upon leaving pool. (?) |
| 7. Adults not secretive; common on roads at night. | 7. *Adults very secretive seldom found even when searched for.* |
| 8. Breed only after violent rains; amount of less significance than rate of fall. | 8. *Breed only after heavy rains; rate of less significance than amount of fall.* |

onic and larval characters as more primitive than adult characters. On the basis of this alone, one would put *hammondii* at the *end* of its phylogenetic line rather than at its base. But one must not forget that larvae as well as adults must live in their native haunts and that this presupposes (at least as a possibility) specific *larval* adaptations to this end. In other words, it may be that the large jaw-muscles and peculiar mandible of the *hammondii* larva are specific larval adaptations and thus of no use in placing this species in its proper relationship to the others. This point awaits further study.

If now we turn again to the reproductive habits of members of the genus *Scaphiopus* and to specific ecological distributions, we find some very interesting phenomena (see also Table 1):

(1) All of Spea and one Scaphiopus (*S. couchii*) are found only in xeric habitats (grasslands of various types and deserts).
(2) All of Scaphiopus (except *couchii*) have more mesic habitats (woodlands, extensive flood plains, and the like).
(3) All species, regardless of their habitat now, show distinctly the xeric reproductive habit-pattern characteristic of desert and grassland anuran life.
(4) But all the genus inhabiting *mesic* environments differ from those which now occupy *xeric* habitats in characteristic ways (more secretive, initial breeding stimulated by heavy rather than violent rains, and perhaps in more delicate response to accumulation of soil moisture and to soil temperature).

These facts are best interpreted as follows (see also Fig. 6):

(1) The genus *Scaphiopus* arose in a xeric environment, presumably in southwestern North America as Tanner suggested.
(2) They lived there sufficiently long to have had the essentials of the xeric breeding-pattern become firmly fixed in their hereditary constitution probably through natural selection.
(3) The first bifurcation of the phylogenetic branch (into the subgenera Scaphiopus and Spea) occurred *before* they left this environmental situation.
(4) Later, all species of the Scaphiopus branch (except *couchii*) spread toward the east and north. In doing so, each changed its habits slightly so that a new sub-pattern tended to be developed in the more mesic situations.
(5) All species of Spea and one species of Scaphiopus (*i.e., couchii*) remained in the original xeric environment and, having found the original habit-pattern good, so to speak, have not changed it materially in the thousands of years intervening.
(6) It follows that (a) the habit-pattern in breeding of any species of this group tends in evolution to adjust the species to some specific environment more or less independently of morphological changes usually interpreted as indicating phylogenetic diversity from other closely related forms; and (b) the suggestion that this general trend is manifested as well by other species (grass-land-limited species of *Bufo, Rana,* etc., as compared with woodland species) makes it reasonable to assume that the xeric-adapted forms of Anura in general have a convergence in habit-pattern more or less cutting across morphological diversities, and therefore, current lines of classification.

Such an interpretation as the above will explain why *S. h. holbrookii* of the East has always appeared so diffi-

cult to understand because it behaves so differently from all other associated frogs and toads. For here is an animal with the breeding habits essentially of a desert-inhabiting anuran, although at present limited to a mesic environment. It also helps to explain why *S. couchii*, although morphologically (both as adult and larva) belonging to the eastern group, is more like the species

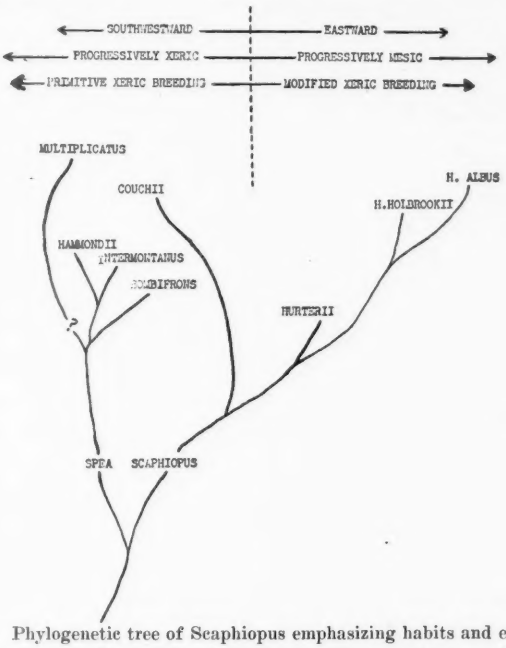


FIG. 6. Phylogenetic tree of Scaphiopus emphasizing habits and ecological relations. Of necessity, such a diagram must be somewhat oversimplified. For details, see text.

of Spea in habits than like its taxonomically closer relatives. This becomes all the more reasonable when we realize one more basic fact, namely, that a xerically adapted frog or toad can live without essential change in reproductive habits in a more mesic environment; whereas, in the reverse situation, the mesically adapted anuran could probably not survive long without change. This must necessarily be so for any animal depending

upon standing water to rear its young, as is the case of most frogs and toads of North America. Any one who has observed at first hand the high plains or the desert country of the North American Southwest under the influence of a summer sun will have no difficulty in appreciating this fact and this is equally true of those who have seen the normal pattern of rainfall in this region, veritable torrents of rain when it does come, filling every hollow with suitable, sometimes quite extensive but always quite temporary, breeding sites. Hurried development of larvae, so characteristically a part of the xeric breeding-pattern as exhibited by the spadefoot toads, is an absolute necessity to the survival in such a rigorous environment whereas this same feature is not a detriment to development in a more mesic situation; hence so little change in Scaphiopus of the East as compared to *S. couchii* and Spea of the Southwest. Carnivorous and cannibalistic tendencies in the tadpoles is another case in point, for the temporary pools formed by the torrential rains of the high plains and deserts are fairly barren when compared with pools of similar extent and volume in more mesic regions, such as the East. This is so, despite assertions of Gilmore (1924) and myself (Bragg, 1940) as to the varied life in such pools because the greater part of this life is of animal nature and all types are in very fierce competition for the few plants which, as always, are the ultimate food source. Partly carnivorous feeding habits are a distinct advantage to any tadpole under such circumstances and this also explains why members of the crustacean genus, *Apus,* a common inhabitant of the temporary pools of the short-grass country, has been seen feeding upon tadpoles of *S. bombifrons,* although it belongs taxonomically to a group usually feeding upon algae. Again, these habits are not particularly detrimental to frogs and toads in mesic situations and so have not been eliminated by natural selection in *S. h. holbrookii* of the East. In fact, as a generalization, it is clear that almost any specialization in habit-detail which

adjusts a frog or toad to a xeric habitat will not be particularly detrimental to it in a moister climate and therefore will not likely be changed by natural selection if the species spreads to, or is introduced into, a more mesic situation. It is equally true that any habit-detail specifically adapting a frog or toad to a mesic habitat tends to serve as a barrier to its spread into a more xeric situation, unless it is able to do so with change toward the xeric pattern. It follows that, the climates of North America being what they are, it is easier for a western species of Anura to move eastward than for an eastern species to extend its range westward on this continent unless advantage be taken of special conditions and special restrictions to quite local ecological situations or unless habits are changed at the right places to be effective for survival.

## Summary

Through seven years, the peculiar advantages of the climate, ecological associations and geographic location of Oklahoma have been used in a study of the habits and distribution of Scaphiopodid toads. Four of the eight known forms occur and every opportunity for their study in all parts of the state has been utilized. Most of this has been in the field at night. Thousands of miles have been traveled and eggs and tadpoles have been studied in the laboratory. This work is here summarized and correlated with that of others in such a way as to form a summary of our knowledge of the group at the present time. The principal conclusions are as follows:

(1) Tanner's (1939) conception of the two species groups as representing two subgenera, Spea of the west and Scaphiopus of the East, is accepted and confirmed by details concerning tadpoles and habits.

(2) Tanner's further conclusion that the Scaphiopodidae arose in the North American Southwest is confirmed, also principally by the study of habits.

(3) It is clear that anuran amphibians in North America which are limited to grasslands and deserts in their distribution have a breeding pattern different from those not so limited. Two principal patterns are described, the xeric and the mesic.

(4) The xeric pattern includes the following tendencies: (a) the lack of a definite breeding season; (b) use of temporary water only; (c)

initiation of breeding behavior in nature only by the coming of rain; (d) a hastened development of larvae; (e) possession of rather loud voice by the male; (f) marked attraction of males as well as of females by the breeding call of the species, thus tending to build up large congresses very quickly.

(5) The mesic pattern includes the opposite tendencies in various degrees and is the common one of eastern species in contrast to those limited to the western grasslands and deserts.

(6) All spadefoots show the xeric pattern exclusively.

(7) However, those in mesic environments vary slightly, but consistently, from those still in xeric environments (*i.e.*, they have developed a subpattern still essentially xeric in nature).

(8) Since a xeric pattern in a mesic environment would not likely be detrimental to the life of a frog or toad, whereas a mesic pattern in a xeric environment in all probability would be, it follows that (other things being equal) eastern forms can spread westward only slowly and with difficulty whereas western species can spread eastward more easily. This, of course, could be modified by other conditions.

(9) Applying these things to the spadefoots, we infer that they arose in a xeric environment, became adjusted nicely to this through natural selection, and split into two subgenera. Then one of these (Scaphiopus) tended to spread eastward and northward (*i.e.*, to mesic conditions), changing in reproduction habits only slightly; whereas the other (Spea) remained in xeric regions without essential change in habits.

(10) The one exception (*S. couchii*) is one that proves the rule; for, although belonging to the subgenus Scaphiopus taxonomically it nevertheless remained in a xeric habitat with members of Spea and retained the original habit-pattern like these.

(11) From this it follows that (so far as North American anuran amphibians are concerned) the habit-pattern in breeding does not necessarily follow taxonomic lines during speciation and dispersal to varied environments. While this is shown most clearly by the spadefoot toads, there is ample evidence of it in other genera as well.

(12) The emphasis in habit-patterns above deals only with similarities; but interspecific differences should not be overlooked. Details given in the text show clearly that each species is different in some respects from all others (even in habits). The situation seems to be that (a) all species differ in details of habits, (b) each tends to be adjusted to reproduce in some one environment or several closely related environments, (c) those inhabiting the same ecological (not necessarily geographic) situation tend (regardless of taxonomy) to develop the same or essentially similar habit-patterns (convergent evolution) and (d) those even closely related taxonomically (and with widely overlapping geographic distribution) which are adjusted to essentially different ecological situations, tend to be different in habits and habit-patterns, even in the same geographic locality.

(13) Spadefoot toads which inhabit the same region (ecologically as well as geographically) tend to be sexually isolated during breeding by two

types of factors, (a) psychological and (b) ecological. Psychological isolation is the more important and is made effective through two phenomena, the differences in behavior of the males in securing mates and the marked interspecific attraction of spadefoot breeding calls. Ecological isolation is only partial and involves differential responses to amounts of rain as well as possible specific selection of breeding sites. The latter may be more psychological than ecological, however, due to the marked attraction for others of the call of the first spadefoot to arrive at a given pool.

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# REVIEWS AND COMMENTS

EDITED BY PROFESSOR CARL L. HUBBS

In these reviews and notices of current biological publications emphasis is given to books and major articles which fall within the special scope of The American Naturalist, in that they deal with the factors of organic evolution. Reviews and Comments are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, Scripps Institution of Oceanography, La Jolla, California. All opinions are those of the reviewer.

**Evolution, Creation, and Science.** By Frank Lewis Marsh. Washington: Review and Herald Publ. Assoc., 1944: 1–304. $2.25.

This book accomplishes what this reviewer believed, before having read it, to be impossible. It would seem that in our day an anti-evolutionist must of necessity be either ignorant of the evidence or incapable of sound reasoning. Yet, this book gives a tolerably readable review of the pertinent facts, and then, by means of what on the surface appears to be sensible argumentation, reaches the conclusion that this evidence favors the theory of special creation and not of evolution. According to "American Men of Science," the author holds a Ph.D. degree from the University of Nebraska; he is also the author of several original investigations published in reputable biological periodicals. But he is convinced that the world and man were created in six days of usual length. The way this legerdemain is accomplished is in itself interesting as an example of high variability of human thinking processes.

The author must be commended for making his premises explicit. To a special creationist, the "approach to biological research must be with impartiality in every point except with regard to those basic principles laid down in the Bible." Among the "basic principles" he

finds that the world began its existence about 6000 years ago; that sometime thereafter all land animals, except those which found refuge in the Ark, were destroyed by a flood; that the now living land animals are all descended from ancestors dispersing from Mount Ararat in Armenia as the center. What a pity that some otherwise efficient intellects are endowed with imagination too shallow to see that great truths can be expressed in poetry and myths!

However, the author rejects the view that all existing species and races were created and placed where they are found to-day. On the contrary, he regards it as established by scientific evidence that great changes and diversification occurred since the flood. What was created were not races or species (the word "species" appears always in quotation marks) but "kinds" (without quotation marks). The definition of "kind" is evidently a crucial matter. We are told that any two forms which are capable of producing a hybrid zygote, even though the hybrid may die in the earliest stages of development, belong to the same "kind," but that failure to cross does not always signify difference in "kind." A "kind" may include not ony several races and species but even genera and families. But in one of the concluding chapters we read "I hold that it is quite impossible to-day to tell which forms are members of an original kind." The reviewer feels that the last sentence contains an implicit blasphemy, for it imputes meanness to a creator who would play such a trick on unsuspecting humanity. Yet, this unsolvable puzzle gives comfort to the author, because it permits him to accept all the evidence experimental biology has to offer for evolution—to him any change is always mere modification within a "kind." In fact, he outbids evolutionists on the score of the speed of the changes, for he assumes that all dogs, foxes, and hyenas are members of a single "kind," and, therefore, must have descended from a common ancestor in any

event less than 6000 years ago. The possible mechanisms of such changes are discreetly left in the dark; the author obviously does not like natural selection, which is not even given a few lines of explanation.

The acceptance of the mysterious "kinds" does not, however, take care of the evidence for evolution derived from comparative morphology, embryology, paleontology and geographic distribution. These problems are dealt with each in a separate chapter, the reading of which perhaps leads one to admire the author's intellectual bravery but does not add much to the attainments of his predecessors in this field. It is, incidentally, surprising that the author ignores the writings of distinguished biologists like Wasmann who have also argued for evolution within but not beyond the limits of variously conceived "kinds." The chapter on paleontology is, as one may expect, particularly startling. Among other interesting things, the reviewer has learned from it about the existence of the periodical named "The Bulletin of Deluge Geology and Related Sciences" which is being published in the United States in the twentieth century (an issue of 1942 is referred to in the book).

A valuable lesson can be derived from reading the book under review. The attractiveness of science to many people lies in that it seems to answer the indestructible yearning for certainty so complete that no thinking mind can evade its acceptance. We like to believe that if we secure adequate data bearing on a scientific problem, then anybody with normal intelligence who takes the trouble to become acquainted with these data will necessarily arrive at the same conclusion regarding the problem in question. We like to speak of conclusions demonstrated, settled, proved and established. It appears, however, that no evidence is powerful enough to force acceptance of a conclusion that is emotionally distasteful.

TH. DOBZHANSKY

**Contributions to the Genetics, Taxonomy and Ecology of Drosophila pseudoobscura and Its Relatives.** By TH. DOBZHANSKY AND CARL EPLING. Carnegie Institution of Washington Publication 554, 1944: i–vi, 1–183, pls. 1–4, 24 figs. $2.25 (paper), $2.75 (cloth).

THROUGH a series of recent researches, among which those of zoologist Dobzhansky and botanist Epling are outstanding, *Drosophila* has been elevated to a position of pre-eminence in speciation as well as in genetics. Such work is effectively filling in the chasms that long split biology into zoology and botany, and each into systematics and genetics, into morphology and physiology, into "closet biology" and "natural history," into observational and experimental subsciences. The way is now being cleared for more unified advances, with more penetrating and more secure attacks on such central problems as evolution.

A skillful combination of genetic experiment and of cytological observations on the giant salivary chromosomes has disclosed races of *Drosophila* that are characterized by different arrangements of the gene-file along one or more chromosomes. It is shown by a brilliant analysis (1) that the several arrangements can be attributed plausibly only to series of inversions and (2) that their phyletic sequences can be postulated with little doubt. This is something distinctly new in a phylogeny that is unsupported by a fossil record. The chromosomal type has been determined for an immense number of individuals representing many populations over western North America and in Mexico and Guatemala. As a consequence it has been possible to analyze the data along several west-east and north-south transects. These exhibit very definite clines, and permit reasonable inferences in regard to the origin and spread of the genetic types.

In two respects such chromosome races appear to have only a limited bearing on the speciation process as it is generally interpreted. In the first place the chromosome

types do not seem to involve other differences, such as might be employed in routine systematics. Secondly, since the chromosomal arrangements are indicated (by a clever statistical analysis) to have little or no selectional significance they are probably not involved in adaptive speciation, which presumably is the usual sort. Nevertheless the thorough analysis of these chromosome types proves very significant.

The chromosome races illustrate beautifully the genetic heterogeneity of species. They are so numerous as to be practically uncountable, occupy very restricted areas and are constantly changing. These and other races are interpreted as genetically open systems through which genes of other conspecific races are free to pass. They are defined in Dobzhanskian style as "populations characterized by different frequencies of the variable genes and chromosome structures."

There appears, however, to be some inconsistency in Dobzhansky's concept of races. After stating that different genes or gene arrangements may flow independently through a species, he asserts that "an individual may, in this sense, belong to two or more races at the same time." But if, as Dobzhansky writes, races are groups of individuals, not single individuals nor single genotypes, then each individual can belong to only one population, except in so far as that population may be split into smaller aggregates or lumped into larger ones. The evolutionary organization of races, by which the characters of each are rendered increasingly uniform and distinctive, appears to be somewhat slighted in studies, like the present one, which are focused on the genetic mechanisms.

With this background of race analysis (written by Dobzhansky) and of the studies on taxonomy, distribution, ecology, dispersal, seasonal cycles and general natural history (worked out by the two authors in collaboration), Epling speculates boldly and interestingly on the ancient history—we might say prehistory—of raciation

in *Drosophila pseudoobscura* and its allies. Leaving an area of solid ground where every concept rests on an abundance of fact, he steps out onto the bog of hypothetical phylogeny. He does not, however, sink wholly out of sight, as many have done on the same ground. Before postulating an historical basis for the present organized pattern of race distribution he plausibly disposes of alternative explanations: wide dispersal by winds, separate origins of each race, and natural selection of chromosome types. Reviewing data on the geological history of the west he abandons the opinion of Dobzhansky and Sturtevant (1938) that the present distribution of *Drosophila* races was determined in relatively recent, perhaps Pleistocene or post-Pleistocene time. Regarding the Glacial climate of the west as having been too much like that of the present to have permitted the establishment of the observed distributional patterns, he dates the origin of races differing only in chromosome arrangement from Miocene or earlier. This seems to me to be an inherently improbable estimate, and my studies of fish distribution in the Great Basin and elsewhere lead to the view that during late Glacial time the whole western region was sufficiently cold (not warm) and moist to allow the establishment then of the present distribution of the *Drosophila* races.

**Speed in Animals.** Their Specialization for Running and Leaping. By A. BRAZIER HOWELL. Chicago: University of Chicago Press, 1944: i–xii, 1–270, figs. 1–55. $4.00.

"SPEED in Animals" is a catch title, obviously designed to help sales rather than to indicate precisely the material treated. The anatomical basis of locomotion in mammals is the real subject. Nothing is included on the speed or on other phases of the locomotion in the invertebrates, which constitute the vast majority of animal species. There is no statement on the maximum speed attained by fishes in swimming, though data are available. The optimum stream-lined form of certain fishes and of other

fast-moving animals is inadequately emphasized. In fact fishes and amphibians are treated primarily as the donors of a structural heritage which limited the locomotor adaptations of the higher vertebrates. Reptiles and birds are likewise accorded only a few pages.

As one might expect from his leadership in the field of the comparative anatomy of the group, the author discusses the locomotion of mammals at much greater length. His prime contribution is a synthesis of mammalian anatomy and behavior. He clarifies the steps by which skeletal and muscular structures were modified in keeping with particular locomotor needs. He thus makes a notable contribution to functional anatomy.

Under "Proportions" there are offered several percentage indices which quantify the relative lengths of parts that are differentially elongated in swift mammals. No indication is given, however, of the variability of the indices within a species.

A particularly detailed treatment is accorded the gaits of mammals, particularly of horses. This section should prove of interest to horsemen.

In general the anatomy and phylogeny of the vertebrates seem to be presented soundly, though only one of two or more conflicting theories is sometimes presented. Occasionally one encounters an incomprehensible suggestion, such as the idea that the abdominal and thoracic pelvic fins of different teleost groups are nonhomologous.

In regard to such controversial subjects as evolutionary processes Howell states that he has followed his own beliefs in preference to presenting all sides of the argument. The seemingly ineradicable ghost of Lamarck repeatedly wafts its way over the pages of the book, as on page 1, where the stimulus for the original formation of the paired fins from scales (a questionable phylogeny) is stated to have probably come from "wriggling over the bottom and between stones in search for food."

NOTICES OF NEW ARTICLES AND BOOKS

**Ends as Well as Means in Life and Evolution.** By EDWIN G. CONKLIN. Trans. N. Y. Acad. Sci., (2) 6, 1944: 125–136.—"I have no theory to propose to explain the origin of organic fitness and human purpose other than the endowment of living beings with differential sensitivity and reactivity, tropisms, organic memory, trial and error behavior, leading in higher animals to intelligence and purpose. . . . But with crude mechanism that finds everything the result of accident and chance I have no more sympathy than with transcendental vitalism. Those who say there are no ends, values, purposes in the living world may understand atoms, molecules and even genes, but they do not understand organisms."

**Geographical Variation in *Rana pipiens* Schreber of Eastern North America.** By JOHN ALEXANDER MOORE. Bull. Am. Mus. Nat. Hist., 82, 1944: 345–370, pls. 61–66, figs. 1–3. $0.60.—With an uncommon degree of thoroughness and precision Dr. Moore has tackled one of the most perplexing problems in the systematics of American amphibians. He demonstrates clearly the inadequacies of prior attempts to separate the *Rana pipiens* complex into species. His work, in fact, is more a critique of previous systematic interpretations than a fresh attempt to define the subspecies—probably many, rather than the two or three customarily considered—into which *pipiens* may prove divisible. His own data, as well as unpublished studies of others, strongly suggest that such local forms can be recognized. A particularly interesting new character brought out in this paper is the usual presence in certain regions of an oviduct in adult males. Chiefly by this feature one might separate a subspecies inhabiting the distinctive faunal area of peninsular Florida. This form is shown to be rather strongly isolated sexually. Other regional differences in biology have been demonstrated by Moore's thorough studies. The existence is suggested of ecotypes on a scale too small and in a pattern too complex to warrant their recognition as subspecies. Since such peculiarities as well as great individual differences seem to dominate the variational picture, Moore makes the thought-provoking suggestion that it would be unwise to delimit subspecies on the basis of the fewer and smaller differences that happen to be correlated with geographical

distribution. There is logic in this unconventional idea, the application of which, however, would spread havoc in systematics.

**A Preliminary Study of the Thermal Requirements of Desert Reptiles.** By RAYMOND BRIDGMAN COWLES AND CHARLES MITCHILL BOGERT. Bull. Am. Mus. Nat. Hist., 83 (5), 1944: 261–296, pls. 19–29, figs. 1–3. $0.70.—Among the conclusions reached in this careful study we may note: The maximum voluntary temperature tolerance of the desert reptiles studied is 42° C., not far below the lethal threshold. Nocturnal reptiles tolerate and prefer lower temperatures than do the diurnal species. Extensive fluctuations are avoided. "Thermoregulation by means of behavior may be considered an element of basic importance in the existence and evolution of reptiles in continental climates." Survival of reptilian relicts on islands and peninsulas is perhaps attributable to the slight temperature fluctuations in maritime climates. "An evolutionary compromise may exist when antagonistic forces are involved."

**The Wolves of Mount McKinley.** By ADOLPH MURIE. Fauna of the National Parks of the United States. Fauna Series, No. 5, 1944: i–xix, 1–238, frontisp., figs. 1–58.—The interrelations of the wolf and the handsome Dall sheep of Mt. McKinley National Park were thoroughly studied from 1939 to 1941 by one of our most capable wildlife researchers. He concludes that the wolves are the main factor in stabilizing the numbers of the mountain sheep; that is, in preventing an overpopulation. The caribou, however, is the main food of the wolf, and serves as a buffer species for the Dall sheep. Evidence is presented to indicate that it is the weak, old and young sheep that are preyed upon. The slowest and weakest caribou calves are the ones that are caught by the wolves. Selection for speed and strength in the young appears to be intense.

"It must be emphasized that national parks are . . . areas dedicated to preserving samples of primitive America," we are told, and Adolph Murie describes such a sample most interestingly. His brother Olaus, an accomplished artist as well as naturalist, has further enlivened the text with his action drawings.

**Ancient Man in North America.** By H. M. WORMINGTON. The Colorado Museum of Natural History [Denver], Popular

Series, No. 4, Second (Revised) Edition, 1944: 1–89, 14 figs. $0.35.—Though written for the comprehension of the interested, intelligent layman, this treatise is so thorough and so judicious as to be of high value to scientists. The conclusion is reached, and seems inevitable on the basis of the scattered evidence here amassed, that man has inhabited North America for at least several thousand years—a much longer period than many anthropologists only a few years ago would have allowed. Indications that the continent was inhabited far earlier than early Postglacial or late Glacial times, however, is discounted. It is particularly clear that sections of the now arid West supported a human population during times when the supply of surface water was much greater and more constant than it now is. At least some of these times were the pluvial periods that are to be synchronized with montane glaciation and very probably with continental glaciation. There can no longer be any reasonable doubt that early Americans were contemporaneous with now extinct mammals long regarded as distinctively Pleistocene. Just when these animals became extinct, however, is admittedly an unsolved problem.

**The Naturalist's Lexicon.** By ROBERT S. WOODS. Pasadena: Abbey Garden Press, 1944: i–xviii, 1–282. $2.75 (7 cents postage.)—With the decline, often the elimination of classical training, scientific names have become to most biologists a mere jumble of letters hard to learn and pronounce. This is particularly true of zoologists, many of whom, even some systematists, accept with equanimity or actually take pride in crude abuses of two inherently beautiful languages. They overuse barbarisms, allow bastard combinations of Greek and Latin and as a rule concoct unnecessarily long, awkward or meaningless names. They miss the pure joy that comes from understanding and especially from coining a name that is short, euphonious and meaningful. Recognizing this state of affairs Mr. Woods has painstakingly prepared for naturalists a manual for scientific names. He starts with a brief but useful discussion of the principles of word formation as applied to systematic nomenclature, then devotes the major portion of the book to a lexicon combining Greek words, arranged according to the Latin transliteration, and Latin words; in all a selection of about 15,000 classical words used or usable in sys-

tematics. He closes with a "Condensed and Classified English-Classical Supplement," arranged primarily as to parts of speech. This last section is potentially the most useful to working systematists, but in the first edition I think is too far condensed to serve the maximum good. I have often felt the need and once started to prepare a more extensive and more thoroughly classified name-finder for those who describe new genera and species. I would have given the combining forms without any separation of the parts of speech. Mr. Woods's book will go far, but a second edition with an expanded classified list would go farther toward the enrichment and refinement of biological nomenclature.

**The Life Energy of Species.** By HAROLD ALEXANDER DANNE. New York: privately printed by author, 131 West 98th St., New York, N. Y., 1944: 1–28, 4 figs. and 1 folded chart (issued in editions bearing on the wrapper such titles as Oil Identification and Wool Identification, differing only in the folded chart). No price stated.—If verified the views of engineer Danne would constitute a revolution in evolution and systematics as well as engineering. By the use of the "Time-energy Cell" and appurtenant apparatus, procurable from the author with directions that are not elaborated in the booklet, it is claimed that one can obtain evidence on "the dynamic origin of species and their composition, growth and propagation." Since water is the carrier of the life energies, the determination of "Hydrol or Moisture" seems to be an important step in the analysis of species.—The whole is quite beyond the comprehension of the reviewer.

**A Life of Travels.** By C. S. RAFINESQUE. Being a verbatim and literatim reprint of the original and only edition (Philadelphia, 1836). Foreword by Elmer D. Merrill. Critical Index by Francis W. Pennell. Chronica Botanica, 8, 1944: 291–360, pls. 5–8, 1 fig. Waltham, Mass., The Chronica Botanica Co.; New York, G. E. Stechert and Co. $2.50.—The brilliant, erratic naturalist Rafinesque will live more clearly in the minds of those who may now, thanks to the editors and publishers, read his autobiography. Through this medium he will invoke in modern naturalists a mixture of understanding, sympathy, pity and humor, as he is followed through his early travels in Europe and his extensive journeys, largely on foot, through the northeastern quarter

of the United States. Again and again he proves what he rather tragically realized, that he was far ahead of his time. Though his reflections were as hasty and erroneous as were his observations, some of his concepts were prophetically brilliant. Thus we learn in the Foreword that as early as 1832 "he forecast the general principles of organic evolution in his published statement: 'The truth is that Species, and perhaps Genera also, are forming in organized beings by gradual deviations of shapes, forms and organs, taking place in the lapse of time. There is a tendency to deviations and mutations through plants and animals by gradual steps at remote irregular periods. This is a part of the great universal law of perpetual mutability in every thing.' "

**Thomas Jefferson and the Scientific Trends of His Time.** By CHARLES A. BROWNE. Chronica Botanica, 8, 1944: 361–424, illustr. Waltham, Mass., Chronica Botanica Co.; New York, G. E. Stechert and Co. $1.25.—Jefferson is pictured as one whose inclinations were more toward science than toward politics, into which he was drawn by the events of his time. His scientific interests were versatile and his effect was great on the development of science in America. His approach to scientific problems was predominantly utilitarian and in his judgment of new scientific ideas he was highly conservative. In fact at times the great champion of human liberty might well have been called a scientific tory.

# SHORTER ARTICLES AND DISCUSSION

## INTERACTION OF ALLELES AT THE BOBBED LOCUS IN DROSOPHILA HYDEI

An analysis of samples taken from *Drosophila hydei* populations has shown that a complex series of alleles occurs at the bobbed locus (Spencer, 1938; in press). During the course of this analysis most of the wild flies tested were mated only to one bobbed tester stock. Such experiments were adequate to demonstrate the genetic variability existing at the bobbed locus, but were not designed to furnish critical evidence on the gene-substrate theory recently developed by Stern (1943; Stern and Schaeffer, 1943; see also Wright, 1941). However, in the course of the bobbed investigation one small experiment was set up, the results of which are of interest in this connection.

Twenty-two males, all phenotypically normal, collected from a citrus dump near Azusa, Southern California, were each mated separately to females from a Wooster bobbed tester stock, the females of which had bristles of grade 20 (posterior scutellars about 400 microns in length); these same males were then mated to females from Berkeley bobbed tester stock, the females of which had bristles of grade 28 (posterior scutellars about 590 microns in length). The maximum bristle grade of females of this species is 33 (posterior scutellars about 690 microns in length).

In Table 1 the results of these tests are given. It will be noted that 7 of the males tested gave phenotypically bobbed daughters with the Wooster grade 20 tester and one of the males gave pheno-

TABLE 1

PHENOTYPIC BOBBED GRADES OF THE HETEROZYGOUS DAUGHTERS OF 22 WILD AZUSA MALES MATED FIRST TO WOOSTER BOBBED 20 FEMALES AND THEN TO BERKELEY BOBBED 28 FEMALES

| Male No. | Bristle grades of daughters from Wooster 20 matings | Bristle grades of daughters from Berkeley 28 matings |
|---|---|---|
| 1 | 30 | 33 |
| 3 | 30 | 33 |
| 14 | 31 | 33 |
| 19 | 31 | 27 |
| 20 | 26 | no offspring |
| 21 | 27 | 33 |
| 22 | 25 | 33 |

Note: All other of the 22 males tested produced daughters with maximum bristle grade 33 in crosses to both testers except No. 10 which gave no offspring in the Berkeley test. Grade 25 has posterior scutellars about 525 microns long and the maximum or normal grade 33 has posterior scutellars about 690 microns long.

typically bobbed daughters with the Berkeley grade 28 tester. The tests of the one male, No. 19, which gave phenotypically bobbed daughters with both Wooster and Berkeley testers do not fall into line with any simple interpretation in terms of heterozygous combinations with intermediate effects. The heterozygote of this wild Azusa gene with the presumably weak bobbed, *i.e.*, nearly normal, Berkeley grade 28 gene is a more extreme bobbed of grade 27 than the heterozygote of grade 31 formed by the Azusa gene and the Wooster grade 20 gene.

This case might well be explained by the gene-substrate interaction theory. In its simplest form this theory postulates two gene properties, one a combining power of the gene with a cellular substrate, and the other an efficiency factor in terms of the utilization of the substrate in the production of a substance for the development of the normal phenotype.

The facts concerning bristle phenotype in this case may be summarized thus, using the symbols $b^W$, $b^B$ and $b^A$ for the Wooster bobbed 20 gene, the Berkeley bobbed 28 gene and the Azusa wild gene respectively:

$b^W\ b^W$ = grade 20 female. $b^W\ b^A$ = grade 31 female.
$b^B\ b^B$ = grade 28 female. $b^B\ b^A$ = grade 27 female.

An interpretation of these facts in terms of gene-substrate interaction offers several possibilities. In the absence of additional information these can not be discriminated from one another. They all agree in attributing relative variations between the alleles in respect to both combining power and efficiency. One of these possible interpretations might be summarized thus:

$b^W$—low combining power; low efficiency.
$b^B$—high combining power; low efficiency.
$b^A$—low combining power; high efficiency.

On these assumptions the heterozygous combination of $b^A$ with $b^W$ would be expected to produce longer bristles than the heterozygous combination of $b^A$ with $b^B$ even though homozygous $b^W$ has shorter bristles than homozygous $b^B$. The other Azusa genes which gave phenotypically bobbed heterozygotes with Wooster bobbed 20 but not with Berkeley bobbed 28 might be thought of as having high combining power and high efficiency. The several heterozygous combinations would then be determined by gradations in the two gene properties interacting to produce the phenotypes observed. It is not likely that either the combining power

or efficiency of a series of alleles can be fully described in terms of only two levels, a high and a low one, but rather by a series of levels including several to many intermediate states between the highest and lowest. A case apparently similar to the one described here has been reported by Goldweber (1939) for allelic interaction at the white locus in *Drosophila melanogaster*.

TABLE 2

MULTIPLE PHENOTYPIC EFFECTS IN THE HETEROZYGOUS DAUGHTERS OF 11 BOBBED FEMALES COLLECTED FROM AZUSA CITRUS DUMP AND MATED TO MALES FROM WOOSTER BOBBED 20 TESTER STOCK

| Female No. | Offspring Sex Bristle grade (n) normal abd. (ab) abnormal | Emergence records Counts at 1–2 day intervals | | | | Viability-Total counts | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Males | Females Higher grade | Females Lower grade |
| h109 | ♂♂ 31 (n) | 9 | 18 | 33 | 35 | 95 | | |
| | ♀♀ 30 (n) | 5 | 5 | 22 | 7 | | 39 | |
| | ♀♀ 14 (n) | | | 8 | 18 | | | 26 |
| h111 | ♂♂ 32 (n) | 10 | 12 | 32 | 14 | 68 | | |
| | ♀♀ 27 (n) | 1 | 12 | 8 | 5 | | 26 | |
| | ♀♀ 19 (n) | | 2 | 12 | 12 | | | 26 |
| h113 | ♂♂ 33 (n) | 12 | 27 | 11 | | 50 | | |
| | ♀♀ 26 (n) | 2 | 7 | 4 | | | 13 | |
| | ♀♀ 13 (ab) | | 2 | 6 | | | | 8 |
| h114 | ♂♂ 30 (n) | 17 | 16 | 25 | 26 | 84 | | |
| | ♀♀ 28 (n) | 8 | 6 | 28 | 10 | | 52 | |
| | ♀♀ 17 (n) | 4 | 0 | 14 | 14 | | | 32 |
| h116 | ♂♂ 30 (n) | 2 | 22 | 37 | 23 | 84 | | |
| | ♀♀ 22 (n) | 1 | 0 | 28 | 19 | | (24) | 48 (24) |
| h117 | ♂♂ 31 (n) | 8 | 17 | 7 | | 32 | | |
| | ♀♀ 18 (n) | 13 | 30 | 4 | | | (23) | 47 (24) |
| h118 | ♂♂ 31 (n) | 19 | 7 | 47 | 24 | 97 | | |
| | ♀♀ 23 (n) | 5 | 8 | 22 | 11 | | 46 | |
| | ♀♀ 12 (ab) | | | 4 | 9 | | | 13 |
| h120 | ♂♂ 30 (n) | 12 | 4 | 31 | 26 | 73 | | |
| | ♀♀ 27 (n) | 2 | 2 | 18 | 6 | | 28 | |
| | ♀♀ 20 (n) | 1 | 3 | 20 | 13 | | | 37 |
| h131 | ♂♂ 31 (n) | 7 | 15 | 36 | 23 | 81 | | |
| | ♀♀ 26 (n) | 2 | 7 | 19 | 7 | | 35 | |
| | ♀♀ 19 (n) | | 7 | 19 | 15 | | | 41 |
| h132 | ♂♂ 32 (n) | 1 | 1 | 26 | 22 | 50 | | |
| | ♀♀ 26 (n) | 2 | 8 | 12 | 7 | | 29 | |
| | ♀♀ 21 (n) | | | 15 | 5 | | | 20 |
| h140 | ♂♂ 30 (n) | 7 | 16 | 29 | 16 | 68 | | |
| | ♀♀ 28 (n) | 1 | 10 | 10 | 9 | | 30 | |
| | ♀♀ 22 (n) | 1 | 5 | 19 | 5 | | | 30 |
| | | | | Totals .. | | ♂♂ 782 | ♀♀ 345 | ♀♀ 281 |

Further evidence that the action of alleles at the bobbed locus in *D. hydei* can not be fully described in terms of a simple potency series with heterozygous combinations showing intermediate phenotypes is derived from a study of pleiotropism at this locus. In Table 2 data are presented on bristle length, condition of abdominal sclerites, emergence time or time of larval-pupal development, and larval-pupal viability among the daughters of 11

phenotypically bobbed females of different grades collected from the Azusa population and mated each to a Wooster bobbed 20 tester male.

Each of the 11 cultures was reared in a large glass vial, using the Kleenex paper-yeast suspension technique described by the author (Spencer, 1943). This culture method ensures a good food supply and uniform culture conditions. However, in some cultures a certain amount of crowding occurred. The best index of this crowding is the size of the sons as determined by the correlated bristle length, which is in the male independent of the bobbed gene carried in the X-chromosome.

All the females listed except h116 and h117 carried two alleles forming phenotypically distinct heterozygotes in combination with Wooster bobbed 20. In general it will be noted that the more extreme of the two bobbed bristle types among the heterozygous daughters in a culture are less viable and have a longer larval-pupal period of development than their sisters. However, the daughters of h117 of the rather extreme grade 18 emerge as soon as do their brothers and appear to be somewhat more viable. While most of the heterozygous combinations listed in the table show normal abdominal sclerites even when of bristle grades as low as 14 the Berkeley bobbed tester of grade 28 referred to above shows abnormal abdomen. It is obvious from these and other observations made on the *D. hydei* bobbed complex that the seriation of various allelic combinations for one phenotypic character is not paralleled by that for certain others. These facts suggest for their explanation assumptions similar to those made by Stern and Schaeffer (1943) in interpreting the multiple effects of certain alleles at the cubitus interruptus locus in *D. melanogaster*.

WARREN P. SPENCER

DEPARTMENT OF ZOOLOGY,
UNIVERSITY OF ROCHESTER

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## THE EFFECT OF REMATINGS ON THE FECUNDITY OF AN INFERTILE MUTANT FEMALE

FEMALES homozygous for *glossy*, an allele of *lozenge* in *Drosophila melanogaster*, are usually sterile. Glossy is a sex-linked recessive trait which is expressed by modification of eye-pigment, abnormal structure of the eye and an absence of the spermathecae and parovaria. Oliver and Green (1944) reported that only 23 per cent. of 899 viable glossy females produced offspring and that those which were fertile produced on the average approximately 9 offspring. The fertile glossy females produced more eggs than offspring. Although they produced offspring only during the first three days following matings, they continued to deposit eggs after that time. Even on the days the females were fecund, many of the eggs failed to hatch. It is apparent, therefore, that for some reason the eggs deposited 72 hours or more after the female has been inseminated do not become fertilized. In so far as can be told by microscopic examinations, the eggs of glossy females do not differ from those of normal females. Glossy females lack two structures of the internal genitalia, the paired spermathecae and parovaria. No visible difference between the ventral receptacle of normal and glossy females can be observed. The suggestion was made by Oliver and Green that the loss of fecundity by glossy females is probably due to a physiological change in the female which causes the stored sperm to lose their ability to fertilize eggs.

Although the eggs produced by glossy females can not upon examination be distinguished from normal eggs, the loss of fecundity by the glossy females might be due to changes in the eggs effected by increased age of the females. Matings have been made to test that possibility. Glossy females were mated, allowed to lose their fecundity, and then mated to another group of males.

Assistance to the study has been given by a grant in aid from the University of Minnesota Graduate School.

### METHODS

Virgin homozygous glossy and wild-type females, not over 48 hours old, were mated individually to wild-type males in vials containing cornmeal-agar culture media. One group of both types of the females was tested to determine how long the females remained fertile after a single mating. After the females had mated, the males were killed. At intervals of 24 hours through a nine-day period, the females were transferred to vials of fresh

media. Counts were made of the offspring produced for each 24-hour period.

Another group of the females was mated first to wild-type males and, subsequently, to Hairless-Moire (*H/Me*) males. Hairless and Moire are dominant traits that are associated with the third pair of chromosomes. Each female was kept with wild-type males for 48 hours. The males were then killed and the female was left in the same vial for three more days. At the end of that time, each female was transferred to a second vial and left for 24 hours. The female was then transferred to a third vial which contained *H/Me* males and was kept with those males for three days. After that period of time, the males were killed and the female was transferred to a fourth vial and kept in that vial for 24 hours. Counts were made of the offspring that each female produced in each of the four culture vials. The four vials represent, respectively, the first five days, the sixth, the seventh through the ninth, and the tenth day after the first mating was made. Offspring resulting from the mating with the first male should be normal (+), except for the glossy character in the males, and those from the second male should show one of the dominant markers *H* or *Me*.

## RESULTS

The results of the tests for the period of reproduction of the wild-type and glossy females are shown in Table 1. Twenty wild-type and eleven glossy females were fertile. Wild-type females produced offspring throughout the nine days of the test and were more fecund than were glossy females. Except for one offspring that occurred on the fifth day after the mating, glossy females produced offspring only in the mating vials, shown as first day in Table 1, and in the vials containing eggs that were deposited on the second and third days after the matings were made. In contrast to the wild-type females, glossy females passed through a brief period of low fecundity and then became sterile. They did not regain their fecundity during the period of the test.

The breeding results with the females that were mated first to wild-type males and seven days later to *H/Me* males are given in Table 2. Offspring produced by the matings with the wild-type males are grouped under the column headed "Before Remating," which is subdivided into two columns; one showing the number of offspring produced in the first vial (first to fifth days of the test) and another giving the number of offspring

TABLE 1

PERIOD OF REPRODUCTION OF GLOSSY AND WILD-TYPE FEMALES FOLLOWING A SINGLE MATING

| Days after mating | | Number of offspring per day | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Female type | Number fertile | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Wild | 20 | 72 | 430 | 661 | 520 | 729 | 415 | 189 | 681 | 269 |
| Glossy | 11 | 7 | 51 | 22 | 0 | 1 | 0 | 0 | 0 | 0 |

produced in the second vial (on the sixth day after the mating). All of the offspring are expected to be normal, (+), with respect to *H* and *Me*. The offspring produced subsequent to the second matings are placed under the column marked "After Remating." The number and kinds of offspring produced for the first three days after the remating are given in the column headed "7th to 9th" days, the latter numbered days referring to the period of time after the first mating. Those offspring produced on the last day of the test are shown in the column marked "10th" day. The kinds of offspring occurring after the remating depend upon the sperm which were stored in the females. Those offspring that were due to sperm from the first males are recorded in the table as "+," and those from the second male are given as "*H–Me*."

Although eight of the wild-type females produced progeny after the matings with both kinds of males, only seven of them still retained functioning sperm from the normal males at the time they were mated to the *H/Me* males. During the last four days of the test the seven females produced both "+" and *H–Me* offspring. The other female that produced offspring with both males had exhausted her supply of functioning sperm from the first male by the seventh day, producing only one "+" off-

TABLE 2

EFFECT OF REMATING ON FECUNDITY AS SHOWN BY THE NUMBER AND KINDS OF OFFSPRING PRODUCED BY WILD-TYPE AND GLOSSY FEMALES

| No. days after first mating | | Before remating | | After remating | | | |
|---|---|---|---|---|---|---|---|
| | | 1st–5th | 6th | 7th–9th | | 10th | |
| Kinds of offspring | | + | + | + | H–Me | + | H–Me |
| Female Type | No. | | | | | | |
| Wild | 7 | 547 | 136 | 220 | 77 | 31 | 72 |
| | 1 | 26 | 1 | 0 | 26 | 0 | 16 |
| | 3 | 168 | 47 | 114 | 0 | 50 | 0 |
| | 3 | 0 | 0 | 0 | 14 | 0 | 19 |
| | 1 | 4 | 0 | 0 | 0 | 0 | 6 |
| Glossy | 9 | 136 | 0 | 0 | 74 | 0 | 2 |
| | 16 | 212 | 0 | 0 | 0 | 0 | 0 |
| | 2 | 0 | 0 | 0 | 15 | 0 | 15 |
| | 38 | 0 | 0 | 0 | 0 | 0 | 0 |

spring on the sixth day, and produced only *H–Me* progeny during the seventh to tenth days. Three normal females were fecund throughout the test but produced no offspring with the second males. Three were sterile with the first males but were fertile after the remating. One female produced only four offspring and those occurred with the first male.

Twenty-five of the 65 tested glossy females were fertile with the first matings. All of them lost their fertility before the second matings were made and, consequently, produced no offspring in the second vial, on the sixth day of the test. After the remating, nine regained their fecundity. However, the second group of offspring were only *H–Me* and, therefore, due entirely to the sperm of the second males. The other sixteen that produced progeny with the first males and lost their fecundity failed to reproduce with the second matings. Two other glossy females produced offspring after the second mating but not with the first. Thirty-eight females were sterile to both matings.

Glossy and normal females differed in their response to the two matings. Normal females that were fertile with the first mating usually retained some of the first supply of sperm through the ten days of the test, and after the second mating the sperm from both males fertilized the eggs. Among the glossy females, 40 of the 65 that were tested produced no offspring with the first male. Even the 25 that were fertile lost their fecundity before the second matings were made. Sixteen of those females failed to reproduce with the second males, but the proportion of females sterile to the second mating is not appreciably higher than the proportion of those sterile to the first mating. The nine glossy females that reproduced with both kinds of males produced only *H–Me* offspring during the second period of fecundity. Yet the fact that they did produce the second group of offspring suggests that the eggs formed in the later period of life of the females can be fertilized.

## DISCUSSION

Females homozygous for the mutant glossy have low fecundity as compared to wild-type females. Many of the glossy females produce no offspring, even though they have been inseminated. Even those which are not sterile produce their offspring only during the first 72 hours after mating.

The failure of glossy females to produce progeny after the third day is not due to any change in the eggs or to the lack of

egg production. That the older females do produce eggs which are capable of being fertilized is shown by the results of a second mating which was made after the females had stopped reproducing (Table 2). Some of the females regained their fecundity when the second group of sperm was supplied. Although some of the females that were fertile with the first males were sterile with the second male, those that did reproduce with both sets of males were approximtely as fecund with the second as with the first males. The nine females produced 136 offspring during the first five days, a daily average of 27, and 74 during the first three days after the remating, a daily average of 25.

It seems probable that, as Oliver and Green have suggested, the loss of fecundity by glossy females is due to a change in motility or viability of the sperm that are stored in the ventral receptacle. Most of the wild-type females retained some of the first supply of sperm throughout the ten days of the test, and after the second mating the sperm from both kinds of males fertilized the eggs. However, none of the breeding glossy females had functioning sperm from the first males at the time the second males were added. After fecundity was reestablished by the second supply of sperm, all the offspring were *H–Me* and therefore due only to the sperm of the second males. Anderson and Oliver (1942) have examined glossy females for the presence of sperm in the genital tracts. They reported that movement of sperm can be observed in the ventral receptacle during the days immediately following matings but not in the older females. Sperm activity, therefore, closely parallels the drop in fecundity found in breeding tests.

A loss of sperm viability was found by Patterson, Stone and Griffin (1942) in their tests of *Drosophila virilis*. Miller (see Dobzhansky, 1941) reported that the sperm of *D. athabasca* retain their viability for a shorter period of time in *D. affinis* than in the receptacles of their own species. Glossy in *D. melanogaster* is a laboratory mutant which seems to have an effect on sperm viability in the tracts of the females within the species.

Although the general picture suggests markedly that the loss of sperm motility is the primary cause of decreased fertility in glossy females, the actual cause of sperm immobility remains unknown. Nonidez studied fertilization in *Drosophila* and suggested that the secretions of the parovarian glands might be necessary for the fertilization process. Other workers have suggested similar ideas (Gleichauf, 1936; Anderson and Oliver,

1942). However, new data that are to be reported by Anderson suggest that the spermathecae may be more important than the parovaria in affecting sperm motility.

## SUMMARY

(1) Homozygous glossy and wild-type females were allowed to mate and then separated from the males. Wild-type females produced offspring through a test period of nine days, but glossy females became sterile by the fourth day and did not regain their fecundity during the period of the test.

(2) Wild-type females that were successfully mated to normal males, and seven days later, to *H/Me* males produced offspring after the second mating that were due to both males. The glossy females that were successfully mated to both kinds of males lost their fecundity before the second males were added and after the second mating produced offspring that were due only to the second males. The sperm stored in the ventral receptacles of the glossy females did not function as long as those in wild-type females, but a second supply of sperm again initiated fecundity in glossy females.

(3) It is concluded that since the eggs produced by glossy females after they have lost their fecundity can be fertilized, the loss of fecundity is not due to changes in the eggs or in egg production. The results support the conclusion that glossy females become sterile due to loss of motility or activity of the sperm that are stored in the ventral receptacle.

C. P. OLIVER
R. C. ANDERSON

UNIVERSITY OF MINNESOTA

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## NOTES ON GRAPHIC BIOMETRIC COMPARISON OF SAMPLES

A PAPER on biometric comparison of samples by Hubbs and Perlmutter[1] appeared while I was on active military service and only recently have I been able to study it. The procedure suggested by them, a modification of the graphic method of Dice and Leraas,[2] is valid and valuable. They do, however, raise two points that demand brief further discussion.

Hubbs and Perlmutter state that Simpson and Roe[3] claim that a different method of computing standard deviation between the differences of means "largely invalidates the Dice-Leraas method of comparing samples or calls for an involved estimate of the reliability of that method when the number of specimens (N) in the two samples is dissimilar." In fact, Dr. Roe and I stated that the Dice-Leraas "method is certainly valid in most cases." We pointed out, however, that the implicit criterion of significance is variable, that under some rather unusual but not negligible circumstances, which were carefully defined and adequately discussed, the results may be misleading, and that when doubt exists calculation of the statistical significance of the difference between means is advisable. What Hubbs and Perlmutter have contributed is, indeed, a method of estimating this significance for certain postulated sample relationships. In our book, previously cited, we gave the same method (in different and, for this particular application, less convenient form), and also methods applicable under other postulates. The apparent slight misunderstanding implied in Hubbs and Perlmutter's criticism of our views is unimportant except that it might arouse misgivings regarding the Dice-Leraas method by suggesting that there is some fundamental disagreement as to its validity under given conditions. The fact is that no such disagreement really exists.

Hubbs and Perlmutter also consider "unwise" our proposal that the values $M \pm 3\sigma$ be indicated on the Dice-Leraas graph, on the grounds that it "clutters the picture and adds little to its interpretive value" and that "extreme limits in the range of variation are hardly predictable in the variable characters of animals." But they have themselves equally cluttered the picture by adding the related values $M \pm 1\sigma$ to the graph, and their

[1] AM. NAT., 76: 582–592, 1942.

[2] Contr. Lab. Vert. Gen., Univ. Mich., 3: 1–3, 1936.

[3] "Quantitative Zoology." New York and London: McGraw-Hill Book Co. 1939.

proposal seems to me to add distinctly less to the graph's interpretive value, for the average zoologist, than does ours. The purpose in each case is to give a measure of dispersion and to suggest the overlap of distributions in the populations represented. As $M \pm 3\sigma$ is both a measure of dispersion and an estimate of population range, it does give some idea of population overlap by a glance at the diagram, and this sort of quick graphic judgment is exactly what a diagram is for. The relation of $M \pm 1\sigma$ to population overlap is less clear and direct.

It is true that the extreme limits of ranges of variation are not predictable in particular cases, but average limits can be estimated and the usefulness of such estimates needs no defense. If only subjectively, every zoologist does make such an estimate every time he compares samples. $M \pm 3\sigma$ is demonstrably a better estimate than is either an observed sample range or a subjective guess as to population range. As a statistical estimate of average tendencies, it is certain that this figure will sometimes be exceeded by the range in real populations and, less often and to smaller extent, in samples. Such cases are not exceptions in the usual sense, but are inherent in the nature of statistical estimation. The theory involved has the same basis as that of standard deviations and standard errors and if the variable biological factors stressed by Hubbs and Perlmutter in this connection were held to invalidate range estimates, they would also invalidate the other methods of comparison supported and proposed by those authors.

Further study has, indeed, shown that estimates of population range even better than $M \pm 3\sigma$ can be made. The defect of $M \pm 3\sigma$ is not that the principle (when correctly understood) is wrong, but that range varies with population size and this statistic is fully consistent only for natural populations of small size (about 450). Formal comparisons of extent of range and adequate studies of range overlap require that these be made on the basis of a conventional standard population size. I have elsewhere[4] discussed this important subject in some detail and have proposed a conventional standard range that is a more useful estimate than $M \pm 3\sigma$. When it is desirable to suggest population dispersions and overlaps on a graph of Dice-Leraas type, inclusion of this standard range is recommended.

GEORGE GAYLORD SIMPSON

THE AMERICAN MUSEUM OF NATURAL HISTORY

[4] Simpson, *Amer. Jour. Sci.*, 239: 785–804, 1941. See also: Simpson and Roe, *Amer. Mus. Novitates*, No. 1190: 1–19, 1942.